

V. *The Anatomy and Morphology of the Leaves and Inflorescences of Welwitschia Mirabilis.*

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[PLATES 17-18.]

TABLE OF CONTENTS.

	Page
Introduction	180
Section I.—The Leaves and Cotyledons	180
A. The Leaf: Adult	180
Two-year-old	182
B. The Cotyledon	183
Section II.—The Inflorescences	184
General.	184
A. The Bracts	184
B. The Male Flower	186
C. The Axis of the Male Cone	190
D. The Naked Axis of the Male Inflorescence	191
E. The Female Flower	194
F. The Axis of the Female Cone	200
G. The Naked Axis of the Female Inflorescence	201
Section III.—Morphology of the Inflorescences	205
A. Branching of the Inflorescences	205
B. Comparison of the Male and Female Inflorescences	206
C. Comparison of the Individual Male and Female Flowers	207
D. Comparison between the Ovules of <i>Welwitschia</i> and some other Gymnosperms	208
Section IV.—Other Points of Theoretical Interest in the Anatomy and Morphology of <i>Welwitschia</i>	211
A. Double Origin of the Bundles supplying the Appendages	211
B. Inversely Orientated and Concentric Bundles	212
C. Centripetal Xylem and Transfusion Tissue	214
Section V.—Relationships of <i>Welwitschia</i>	215
A. General Remarks	215
B. Comparison between <i>Welwitschia</i> and the Cycads	215
C. Comparison between <i>Welwitschia</i> and the Bennettitales	217
D. Comparison between the Gnetales and the Angiosperms	218
Section VI.—Summary and Conclusions	219
Bibliography	222
Description of Plates	225
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INTRODUCTION.

ALTHOUGH the structure of *Welwitschia* has already been investigated by various workers,* it seemed advisable that this interesting and isolated genus should be further studied in the light of recent knowledge. At the suggestion of Prof. SEWARD I undertook this study, and material was kindly sent by Prof. PEARSON, of Cape Town. This material consisted of plants probably more than 20 years old, the stems of which were about $2\frac{1}{2}$ inches in diameter, and inflorescences. The male inflorescences contained flowers in all stages of growth; but in the oldest female flowers the ovule was still very immature, and the embryo not yet developed. I also received two seedlings, one 13 and the other 27 months old, from the Cambridge Botanic Garden.

This research has been carried out in the Cambridge University Botany School during my tenure of a Bathurst Studentship (1908-9) and a Newnham College Fellowship (1909-10).

SECTION I.—THE LEAVES AND COTYLEDONS.

A. *The Leaf.*

The adult foliage leaf† is isobilateral, and has many striking adaptations to xerophilous life. Both epidermal layers (fig. 2, Plate 17) are composed of cells with strongly thickened outer walls, and the deeply sunk stomata are arranged in parallel rows. The outer wall of each epidermal cell is composed of three distinct layers, and is also incrustated with a small deposit of crystals of calcium oxalate. The innermost layer (C, fig. 2, Plate 17) stains deeply with cellulose stains; the middle layer is (B, fig. 2) of considerable thickness, is slightly cuticularised, does not stain with cellulose stains, and is impregnated throughout with minute crystals of calcium oxalate;‡ the outermost layer (A, fig. 2) is much thinner, it does not react to cellulose or cuticular stains, and projects at the corners of the cells through the middle layer, and touches the inner cellulose wall.§

The stomata|| have subsidiary cells, and are deeply sunk at the bottom of a chamber formed by the cells of the epidermis (figs. 2 and 3, Plate 17). When a portion of the leaf is incinerated not too strongly, these holes are clearly obvious in the skeleton of calcium carbonate which is thus obtained. The guard-cells of the stoma (figs. 2 and 3, Plate 17) are each provided with a strong median cuticularised ridge (R in figure) running at right angles to the long axis of the stoma; they are also slightly

* HOOKER, 1863; STRASBURGER, 1879; BOWER, 1881; DE BARY, 1884, etc.

† DE BARY, fig. 187, p. 408; fig. 145, p. 303; fig. 157, p. 335; STRASBURGER, 'Leitungsbahnen,' pp. 150-157.

‡ DE BARY, pp. 141, 132; SOLMS LAUBACH, 1871, pp. 541-542.

§ Cf. HABERLANDT (Aloe), p. 66, fig. 21a.

|| SOLMS LAUBACH, *loc. cit.*, fig. 20, Taf. 6.

cuticularised round the mouth of the stoma (M), and have smaller cuticularised ridges (Z, figs. 2 and 3, Plate 17) on their bases over part of the area by which they abut on the small respiratory cavity; thus, the only areas left uncuticularised in the wall of each guard-cell are a portion at the base, which is in contact with the respiratory cavity (X, figs. 2 and 3, Plate 17), and two longitudinal ridges (Y, figs. 2 and 3), where the wall is, however, slightly thickened, and where it is in contact with the wall of the subsidiary cell.*

The small respiratory cavity under each stoma is bounded on its inner side by the palisade tissue, which is composed of thin-walled cells much elongated in a direction at right angles to the surface of the leaf, and which, except at this point, rarely reaches the level of the epidermis. Directly under the epidermis are strands composed of elongated fibres,† with thick, but unlignified walls, running parallel to the long axis of the leaf; between these strands small groups of isodiametric cells with lignified walls are often found.

The centre of the leaf is occupied by a thin-walled parenchyma with small crystals in its intercellular spaces;‡ this tissue probably serves for water storage. Small strands of the sclerenchymatous fibres referred to in the hypoderm are found in this tissue, and a few mucilage glands§ occasionally appear on the lower side of the leaf; large numbers of the remarkable branched "spicular" cells|| occur in all regions of the leaf, some of them extending from this central tissue to the epidermis, under which they generally terminate in a hook. The spicular cells have a narrow cavity, a thick inner lignified and a thinner outer cellulose wall; in the latter, numerous large crystals of calcium oxalate are found.¶ The wide distribution of crystals throughout the leaf and other regions of *Welwitschia* is commented upon by all observers; the crystals were found by SOLMS LAUBACH to be calcium oxalate.**

The vascular system, confined to the central mesophyll, consists of a number of similar parallel bundles, which at intervals give off small branches. As a rule, two of these branchlets arise simultaneously from two neighbouring bundles, and, converging obliquely towards one another, fuse; the single bundle thus formed then runs back a short distance towards the base of the leaf, and ends blindly in the mesophyll. More rarely, one of the smaller bundles arises at a different level from the other,†† or two lateral branches from one bundle fuse with a single branch of a neighbouring bundle. The larger bundles are often found to give off these secondary anastomosing

* Cf. SPRECHER's figure of the stoma in *Ginkgo*, 1907, p. 75, fig. 81.

† DE BARY, p. 420.

‡ DE BARY, p. 335.

§ Cf. BERTRAND, 1874, p. 17.

|| HOOKER, 1863, p. 12, Plate 13, figs. 5-8; DE BARY, pp. 132-3, fig. 55; SOLMS LAUBACH, 1871, p. 526. Cf. *Sciadopitys*, *Agathis*, *Araucaria imbricata*, etc., also *Gnetum* (DE BARY, p. 130).

¶ For the development of these cells see BOWER (2), p. 590.

** SOLMS LAUBACH, 1871, pp. 521, 526-529, 541.

†† Cf. DE BARY, fig. 145, p. 303.

traces at the same level, so that in some cross-sections no sign of branching can be found.

Each large bundle is normally orientated and is surrounded by a well developed sheath of isodiametric or slightly elongated transfusion tracheides with lignified walls and simple or elongated pits (figs. 1 and 4, Plate 17). The pericycle is composed of elongated cells with large nuclei. Both above and below the bundle is a large group of thick-walled unligified fibres, similar to those found in the hypoderm. The bundle grows in thickness by means of a cambium. The primary phloem is much crushed and hardly recognisable; the secondary phloem consists chiefly of sieve tubes, with sieve plates on their lateral and terminal walls, and of phloem parenchyma.* The protoxylem, owing to the long continued growth of the leaf, is stretched and contorted. It is composed of tracheides with a much extended spiral or annular thickening, surrounded by a large number of parenchymatous and unligified cells.† Sometimes some of the cells surrounding it have been converted into fibres, in which case it has not collapsed as completely (fig. 4, Plate 17) as in cases where it abuts only on thin-walled cells.

The later formed xylem is disposed in radial rows separated by medullary rays of unligified parenchyma, and consists chiefly of tracheides, the diameter of the younger tracheides being many times that of the first formed elements. The walls of the narrowest tracheides often have both spiral thickenings and bordered pits, others have uni- or multi-seriate bordered pits alone; many of the larger tracheides have a simple reticulate pitting, and in the largest elements the oblique end walls have large simple pits.††

The small anastomosing strands are similar, even in the possession of secondary thickening, to the large bundles. Their xylem is chiefly composed of reticulate tracheides, and no spirally thickened protoxylem elements are present; the sheath of transfusion tissue which accompanies the bundle is sometimes extended by means of scattered elements for some distance into the ground tissue, and would seem to take the place physiologically of further branching of the xylem elements.

The leaf of the two-year old plant§ differed very little from the adult leaf, save in size and in the number of its bundles.

The series of parallel bundles, derived from the pair primarily supplying each leaf,|| already consists of from 10 to 11 bundles, and is being further increased by numerous small bundles intercalated between the primary series and produced from the meristematic tissue at the base of the leaf. A small number of new bundles have

* BERTRAND, p. 16.

† DE BARY, p. 334.

‡ BERTRAND, p. 16. Similar elements are found in *Ephedra*, while in *Gnetum* the transverse wall of one of these large xylem elements has often only one large simple pit.

§ Cambridge Botanic Garden, 1907-1908.

|| BOWER (1), p. 22.

also arisen towards the edges of the leaf, but this process soon ceases,* and bundles are only added in the later stages by intercalation at the base. A study of the seedling anatomy† shows that it is largely to this remarkable method of leaf supply that the chief peculiarities of the vascular system of *Welwitschia* are due; in its early stages it differs in no important point from *Ephedra*.

As yet the spicular cells were undeveloped, but large masses of sclerenchyma were already differentiated under the epidermis. No deposit of calcium oxalate was yet found on the surface of the epidermis. Many of the bundles had already an incomplete sheath of transfusion tissue, the elements of which showed all stages in the lignification of their walls.‡ Sclerenchyma was differentiated on the phloem side of the younger bundles, but on both sides of the older bundles the anastomosing bundles were as yet few and irregular, and blind prolongations were infrequent.

B. *The Cotyledon.*

The cotyledon, like the foliage leaf, is isobilateral, and has stomata and palisade tissue on both sides. The epidermis consists of cells whose outer thickened walls are composed of two layers, an inner cellulose and an outer thickened crystalline layer. No bundles of sclerenchymatous fibres and very few spicular cells are found, otherwise the ground tissue is as described for the foliage leaf. Two main bundles enter the cotyledon§ and branch in its base to form a parallel series, which extends to the tip but does not give rise to lateral blind or anastomosing strands. Each bundle (fig. 7, Plate 17) has a very incomplete sheath of lignified elements, and no masses of sclerenchymatous fibres protect the vascular tissue. A small amount of secondary growth by means of a cambium takes place, and the elements produced are similar to, though simpler than, those found in the foliage leaf.

At the base of the cotyledon a few isodiametric, reticulately pitted tracheides are developed on the centripetal side of the protoxylem of each bundle; these tracheides are connected with the epicotyledonary bundles, and it does not seem clear that they are homologous with the centripetal xylem of the Cycads and other Gymnosperms. Higher up in the cotyledon the bundles have no trace of anything of the nature of centripetal elements.

No transfusion tissue was present in connection with any of the bundles traversing the cotyledon of a 13 months old seedling, and very little was developed even at two years old||; consequently, it was not possible to ascertain whether there be any connection between this tissue and the centripetal xylem. The few elements of

* BOWER (2), p. 586.

† BOWER (1) and (2); SYKES, Linn. Soc., May 21, 1910; Linn. Trans. (*in ed.*).

‡ In the leaf of a one-year-old plant no transfusion tissue was yet developed in connection with the bundles, the whole structure resembling that of the cotyledon.

§ BOWER, pp. 21-23.

|| At this age the cotyledons are beginning to wither.

transfusion tissue developed in the old cotyledon are situated in the pericycle, chiefly on the phloem side of the bundle (fig. 7, Plate 17).

SECTION 2.—THE INFLORESCENCES.*

An account of the grosser morphology of the inflorescences has lately been published,† and it will therefore be necessary to recapitulate here only the main points.

The male and female inflorescences, bearing the cones, are both branched dichasially, and are bare of appendages, except at the points of branching. In the typical inflorescence the primary and secondary axes terminate in cones. Just below each cone are two lateral branches in the axils of two opposite bracts. In the male inflorescence the branching is several times repeated, and the lateral branches, like the primary axis, generally terminate in cones, below which again occur two opposite bracts with axillary branches or cones. The female is less branched, and occasionally may even bear but a single cone. In this case, as often in the terminal cones, the two bracts are present, but the lateral branches are represented only by aborted axillary buds.

The cones thus occur at the forks, or at the ends of the ultimate branches. The male cone is composed of a large number of decussate bracts, in the axils of all but the lowest two or four of which are single, almost sessile male flowers. The female cone, which is much larger, bears first a number of sterile bracts, and above these the fertile bracts, each subtending a shortly stalked female flower.

A. *The Bracts.*‡

The two bracts occurring at the point of branching of the inflorescence are narrower and more pointed, but in all respects similar in structure to the adult bracts of the cones, which have been more fully investigated, and to which this description more especially applies.

The adult bracts of the cones are highly differentiated, but differ in many respects from the foliage leaves. Each bract consists of a thick median portion, with two membranous wings (fig. 5, Plate 17). It is supplied by a pair of vascular bundles, which are from the beginning widely separated, and diverge still further during their course in the bract. These two bundles run along the periphery of the thicker median portion of the bract, and branch at intervals, the branches always bending towards the centre of the bract. The branching of the two main bundles is

* In a description of the inflorescence it is necessary to use certain descriptive terms, but I do not wish them to be considered as bearing a morphological meaning. Thus I have called the bare portion of the axis, the peduncle; the cones or aggregates of cones, the inflorescence; and the structures in the axils of the cone-bracts, flowers.

† PEARSON, 1906, 1909.

‡ STRASBURGER, 1872, p. 94, Taf. 18, fig. 25.

dichotomous;* so is most of the branching throughout the bract; only occasionally have bundles been seen to branch into three. The course of the two systems of bundles on either side of the bract is strikingly symmetrical. No bundles whatever are given off towards the wings, which consist mainly of thick-walled fibres enclosed in an upper and lower epidermis.

A large number of mucilage canals are present: these are especially well developed in the bracts of the female cone, and in all the bracts are chiefly confined to the central part of the thicker portion of the bract, in which no vascular bundles are formed. The presence of these mucilage cavities makes the detached or broken bracts sticky. In the female cone the developing seed is closely appressed to this central non-vascular portion of the bract, and in some of the oldest material which I examined a hole had been formed in this region of the bract by mucilaginous degeneration; into this hole fits the developing seed, which in life was thus kept moist.

In the younger cones all the bracts are composed of thin-walled tissue, and the vascular bundles are simple and collateral,† consisting of a few rows of phloem elements and a horseshoe-shaped mass of xylem, the tissue between the xylem and phloem being in active division. In the oldest female cone which I examined, the base and central portion of the fertile bract was still in this stage; but the tips of the fertile bracts, and a large portion of the sterile bracts, like the whole of the bracts of the male, were considerably more differentiated. A longitudinal section of an older female cone shows very well the bract base composed of thin-walled elements and the protective bract apices with their well-developed mechanical tissue.

The thicker portion of the old bracts consists of from eight to ten layers of cells, and is composed chiefly of isodiametric cells thickened at the corners. The bract is not isobilateral like the foliage-leaves. Its outer or dorsal epidermis is composed of columnar cells, the walls of which consist of thickened but uncuticularised cellulose. The stomata are fairly numerous, they (fig. 9, Plate 17) are not so deeply sunk as those of the leaf. The guard-cells are cuticularised round the pore, and have also two prominent median cuticularised ridges, but they have no basal ridges; thus large portions of the walls which abut on the subsidiary cells and on the respiratory cavity are uncuticularised. Under the outer epidermis occur a very large number of branched cells with their walls lignified, but without crystalline deposits. These are very well developed in the old sterile bracts of the female cone, where they form a definite layer, the branches of which may, however, extend for some distance into the mesophyll. These branched cells are developed even in the non-vascular central portion of the female bract, where they are the only lignified tissue. They are also sparsely distributed throughout the mesophyll of all portions of the bract.

There is no palisade tissue. The inner epidermis, that turned towards the cone

* Compare with the dichotomous branching of the bundles in the sporophylls of Cycads; see WORSDELL, 1898, fig. 5, Plate 17.

† The bracts examined by both STRASBURGER (1872) and PEARSON (1909) appear to have been in this stage.

axis, is composed of flattened and thin-walled cells, and I have seen no stomata in this layer. A well marked hypodermal layer of sclerenchymatous fibres is found on this side of the bract.

The bundles (fig. 8, Plate 17) are collateral, as in the young bract: they are surrounded by a well-developed but not continuous sheath of isodiametric or slightly elongated transfusion cells, with lignified and reticulately pitted walls. The bundles also, towards the apex of the bract, terminate in a group of transfusion cells. From the ground-tissue are developed at frequent intervals similar large isodiametric cells, which extend from the transfusion tissue immediately around the bundles, and form a widely spread water-conducting system. These cells are especially well developed in the bracts of the male cone.

Various stages in the development of the bundle of the young bracts have been studied.* It was found that in a few cases near the apex of the male cone the transfusion-tissue elements in the mesophyll were lignified before the xylem, but this was unusual, and even here the sheath of transfusion elements round the bundle arises later. Usually the xylem is lignified first, and the transfusion tissue is developed later. The order of lignification of the xylem elements is not very regular. In the bracts of the female cone studied, the xylem was generally all centrifugal. In those of the male cone, it was often noticed that a laterally disposed element became lignified first and that the later developed elements extended from it in a more or less straight line parallel to the surface of the bract.† Occasionally a few xylem elements are centripetally developed, but this fact has probably no significance. In the next stage transfusion tracheides are developed outside the phloem,‡ and give the bundle a concentric appearance in transverse section, but later still a complete ring of lignified elements surrounds both the xylem and phloem of the collateral bundle.

In the young bract, the hypoderm of sclerenchyma under the inner epidermis is formed early, but the branched and lignified cells under the outer epidermis do not arise till later. It is also at this later stage that the cuticular ridges on the stomata are developed.

B. *Male Flower.*

The flower consists of an outer whorl of two small bracts, an inner whorl of two more expanded but similar bracts, six stamens coherent by their bases, and a small abortive ovule in the centre, consisting of a solid central body, with a single integument prolonged into a flaring expansion.

The *bracts* have no stomata and no vascular supply. They are membranous and

* An early stage has been figured by STRASBURGER, 1872, Taf. 20, figs. 47, 48, and described by PEARSON (1909, p. 340). Neither of them appears to have recognised that they were dealing with immature structures.

† Cf. BOWER (1), description of the young hypocotyl, p. 20, fig. 13, Plate 3.

‡ Cf. SCHEIT, who considers the origin of transfusion tissue in the Gnetaceæ to lie always in the xylem. *Ex.* WORSDELL, 1897, p. 303.

resemble in structure the winged portion of the protective bract; the members of the inner whorl consist generally of about three layers of cells, of which the central layer is chiefly composed of sclerenchymatous fibres; the bracts of the outer whorl are made up of a larger number of layers of cells, amongst which many sclerenchymatous and lignified fibres are to be found.

The coherent bases of the two large and four smaller *stamens* are made up of thin-walled starchy parenchyma, and each stamen receives a single concentric vascular bundle,* containing 8 to 10 xylem elements surrounded near their termination by a narrow ill-defined layer of phloem-like tissue, which broadens out at their base and merges gradually into the cortical parenchyma (figs. 14, 15, 16, Plate 18). The xylem is chiefly composed of reticulate and bordered pitted tracheides. The phloem is much reduced in structure and does not appear to contain any sieve tubes, but is composed of elongated parenchymatous cells with dense contents and large nuclei. Each trace ends at the base of the anther, between the three pollen-sacs, in a large mass of cells with strongly lignified and reticulately pitted walls resembling the transfusion sheath of the leaf bundle and prolonged beyond the termination of the trace† (figs. 13 and 16, Plate 18).

The *integument* is composed of about three layers of cells, many of the elements of the middle layer having thickened or lignified walls; it has no vascular supply.

Although so many parts of the male flower receive no vascular supply *the course of the bundles*‡ in the flower axis is not by any means simple and appears to me to represent the reduced remains of a more advanced structure. A pair of vascular bundles arises from the cone axis in the manner described below;§ at their origin the xylem of each is directed towards the centre of the stem axis, but in their progress through the cortex it rotates through three-fourths of a circle (Dia. II, A, B, C; *a*). As the bundles approach, their phloems turn towards one another, and their xylems turn outwards, towards the circumference of the stem (Dia. II, B); finally the xylems point towards and the phloems away from one another (Dia. II, C). The two bundles almost immediately divide, each into three portions,|| and hence a whorl of six bundles is found in the flower stalk. The middle bundle of each trio passes out to supply one of the two largest stamen filaments.

The two anterior bundles, those furthest from the main axis, now approach one another and become connected by a cambium (Dia. II, E); the sides of the mass thus formed then become detached and supply two more staminal traces (Dia. II, E, *II*), sometimes leaving also a minute portion in the flower axis (not seen in this series of

* Compare with bundles of Bennettites seed pedicel and intraseminal scales, WIELAND, G. R., fig. 61, B, and pp. 119–120. See WORSDELL, W. C., 1901, p. 767.

† These cells recall the transfusion tracheides commonly found at the termination of the trace supplying the receptacle of a fern sorus.

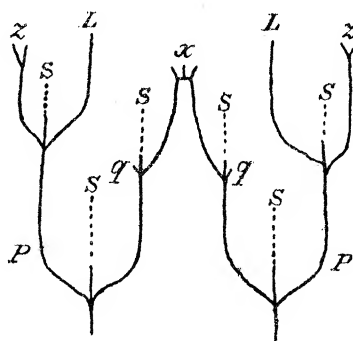
‡ STRASBURGER, 1872, pp. 145–147, figs. 41–43.

§ Page 11, Dia. II, A—C (*a*).

|| STRASBURGER, 1872, p. 145.

diagrams but see Dia. I, *q*, and figs. 17, 18, Plate 18), meanwhile the median portion sometimes dies away at once, is sometimes prolonged for a little distance, or may even form an extended plexus, in which, however, but little lignified tissue is found (Dia. II, F, G; *X*).

The two posterior bundles, those nearest to the cone axis, also approach each other (Dia. II, E, 2); they each give off a small bundle on their adjacent side and these small bundles become connected with each other and with the larger portions by radial rows of thin-walled cells derived from a cambium. The two larger portions at once divide again, one product of each division forming a staminal trace. Thus the two posterior bundles divide each into three, the centre bundle of each trio passing out to a stamen, the two lateral ones remaining in the flower axis (see figs. 14 and 15, Plate 18, and Dia. II, G, L).



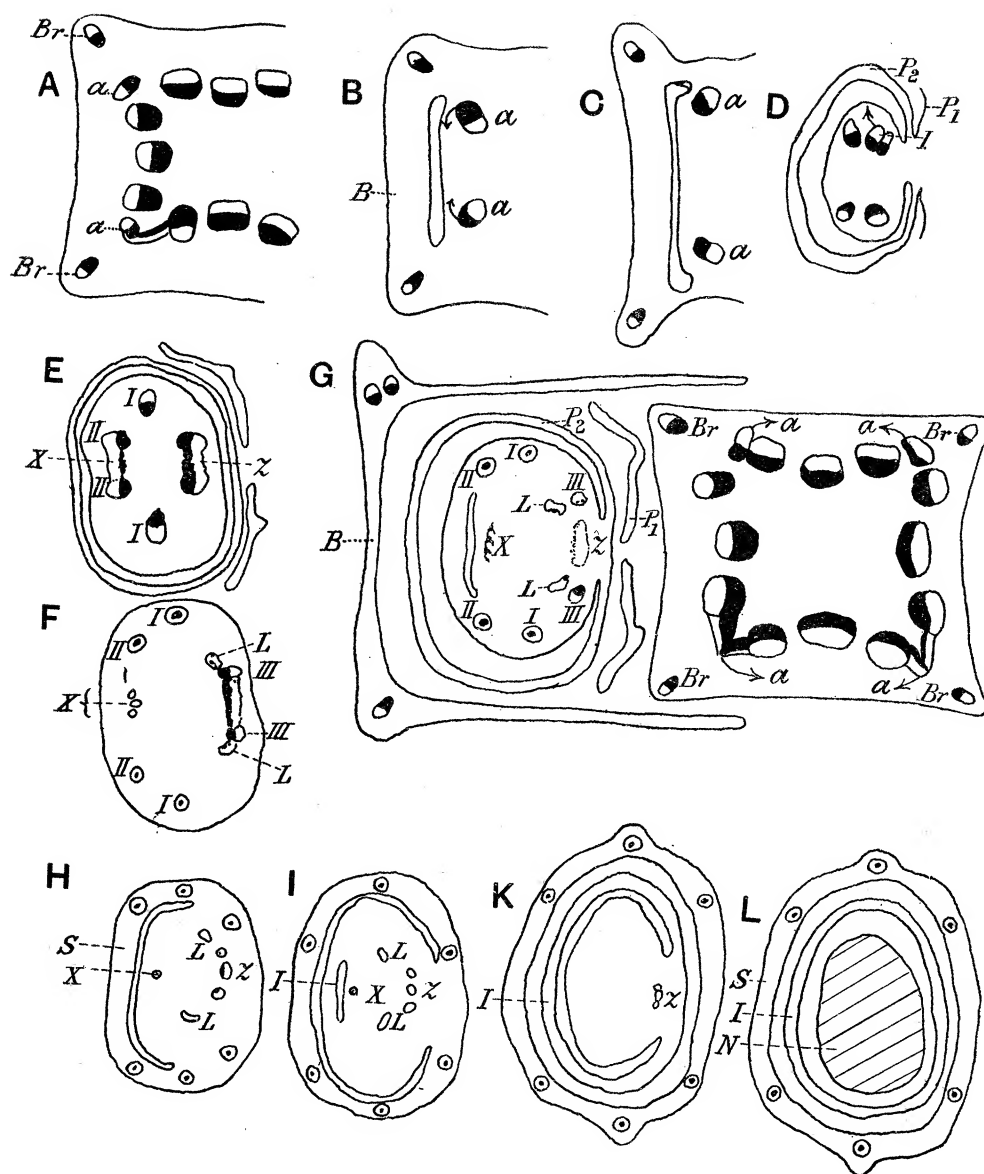
DIA. I.—Course of Bundles in Male Flower.

S, trace supplying stamen. *P, P*, posterior pair of bundles (*i.e.*, those nearest main axis). *L, L*, two most prominent bundles of perinucllary ring (corresponding to *L, L*, in ♀ flower axis, *i.e.* the bundles which supply the outer integument, and which arise, like these, from the posterior main pair.) *q*, additional bundle formed at branching of anterior bundles.

(Compare with Dia. IX, 3, p. 197, of female flower. It will be seen that the course of the bundles is similar in both cases, the main difference being caused by the six bundles which supply the stamens, and which are as if inserted on to the bundle system in the male flower, each stamen trace arising from the points of forking of the main bundles.)

This method of division is similar to that followed by the two main bundles of the flower. Each division may be compared to a dichasial sympodium, of which the median terminal portion is used up as a sporangiophore supply, while the two lateral portions run on in the flower axis (Dia. I). The method of division of the anterior pair of bundles is more variable.

After the staminal whorl has become detached a ring of bundles is left in the flower axis. This ring consists of one, two, or three faintly differentiated bundles on the anterior side (Dia. II, *X*) (sometimes also flanked by two minute bundles left after the departure of the two anterior stamens), and a fairly well differentiated posterior mass of vascular tissue, consisting of from one to three bundles (Dia. II, *II*), and two large lateral bundles (Dia. II, F, G, H; *L*), derived also from the posterior pair and



DIA. II, A-L.—Series (slightly oblique) through Male Flower.

P_1 , P_2 , non-vascular bracts. S , whorl of stamen bases. I , integument. N , nucellus. B , bract. Br , traces supplying bract. a , traces supplying flower stalk. I , II , III , traces supplying stamens. X , portion of perinucellary ring which is derived from the two anterior bundles. Z , portion of perinucellary ring which is derived from the two posterior bundles. L , the two most prominent bundles in flower axis, derived from Z and dying out at the base of the integument. (Black, xylem.)

standing somewhat outside the ring.* These two bundles are very noticeable: both because of their position, and because of their origin from the posterior bundles. I am inclined to regard them as homologous with the two bundles which form the vascular supply of the outer covering of the female flower, and which, as in Dia. IX, 3, sometimes arise similarly from the posterior bundles. The remaining bundles of the flower axis appear to represent the reduced remains of the perinucllary ring of bundles of the female flower.

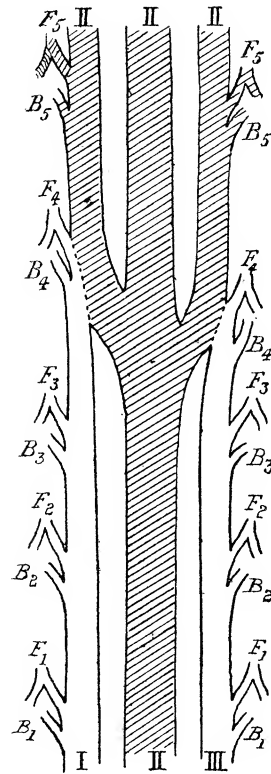
C. *Axis of Male Cone.*

The axis of the cone is made up of parenchymatous ground tissue, in which sclerenchymatous fibres are scattered. Mucilage cavities occur in the cortex, and are continuous with those of the bracts. The vascular system consists of four groups of three or four bundles each, corresponding to the four rows of bracts, and forming a quadrangular stele. Each bundle grows in thickness by means of a cambium; the xylem is largely made up of tracheides with spiral thickening, or spiral thickening and bordered pits, or uniseriate bordered pits only; there is no sheath of transfusion tissue as in the leaf bundle.†

The bundles of each group are arranged in a half-moon (Dia. II, A, G); the two opposite groups are generally in almost the same stage at any given level. At the origin of a bract, the two corner bundles of the corresponding main group each give rise to a trace, which, without torsion, passes straight out to the periphery (Dia. II, G, *Br*, p. 189). The origin of the two bundles supplying the axillary flower stalk varies: one or both may have a simple origin from a corner bundle of the group; but more commonly both have a double origin, one half being formed by the branching of the corner bundle of the group (the same bundle which has just provided one of the bract traces), and the other half by the branching of the adjacent corner bundle of the next group (Dia. II, G, *a*); occasionally, near the cone-apex, the flower bundles originate simply from the corner bundle of the adjoining group. It will be seen from the above description that the corner bundles of the groups are alone concerned in the production of lateral traces. For some time the same corner bundle may run on in the axis, supplying traces to bracts and flowers. Sooner or later it becomes used up in this process, and passes out entire. This occurred at the fifth whorl of flowers in one cone which was examined, and was seen to happen at intervals in all four groups. Its place is then supplied in the cone-axis, and the normal number of bundles restored, by the branching of one of the others, a new corner bundle being thus formed, which now takes part in the supply of bracts and flowers (Dia. III). Thus, in turn, each of the bundles in the cone-axis takes part in the formation of foliar and flower traces, and none of them is entirely cauline.

* STRASBURGER, 1872, p. 146, remarks on these two bundles and suggests that they have the appearance of being about to supply "a pair of foliar segments."

† STRASBURGER, 1872, pp. 144-145.



DIA. III illustrates the course of one of the four groups of vascular bundles in the base of the axis of a male cone. It is constructed from a series of transverse sections. I, II, III, the three bundles of a group. Three bract traces (B_1 – B_3) and three flower traces (F_1 – F_3) are formed in the normal manner. Each flower trace is joined by a small trace from the corner bundle of the next group. The bundles I and III are used up in the formation of the fourth flower and bract traces. Bundle II then branches to fill their places.

D. *Naked Inflorescence Axis (Male).*

The naked axis has an epidermis which is slightly cuticularised, and in which stomata are sparsely distributed, occurring chiefly just beneath the bracts at the points of forking. The cortex is composed of thin-walled cells, interspersed with numerous groups of sclerenchymatous fibres; below the bracts occur lignified branching fibres and mucilage-containing canals. The whole of the pith is lignified, and consists of elongated cells with reticulately pitted walls.

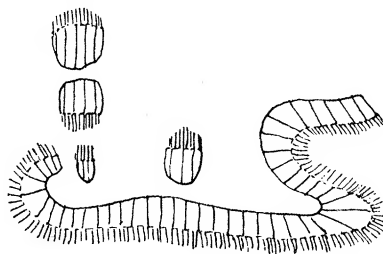
The extremely complex and variable character of the vascular system in the naked axes of both male and female inflorescences makes its investigation a long and tedious process.

At the base of the "peduncle" there are two irregular whorls of bundles. The vascular tissue, here and throughout the inflorescences and flowers, appears to be all derived from the divisions of a cambium, all the elements being arranged in radial rows. A group of small lignified cells is present on the centripetal side of the xylem,

and merges gradually into the lignified pith.* Higher up in the peduncle, a few fibres are occasionally present on both sides of the bundle.

In the terminal branches of the inflorescence the number of bundles is reduced, and those in the outer whorl alternate more or less clearly with those of the inner.† In the ultimate branch of one inflorescence, at a level of 1 inch from the apex, 13 bundles were present in the inner ring and about 15 in the outer, while three others occupied a more or less intermediate position between the two rings.

The course of the bundles entering the apex of the peduncle will be described from above downwards. At the base of the cone the arrangement of the bundles in a square (pp. 189–190; Dia. II, G) is lost and a single ring is formed. The bundles of this ring are no longer collateral, but become *inversely concentric*‡ by the folding together of the two ends of the cambium over the phloem. This amphivasal§ arrangement is very common throughout the naked axis, and is especially prevalent in the bundles which form the inner whorl.|| At the extreme base of the cone a few inversely orientated bundles appear on the outer side of the main bundles



DIA. IV.—Single bundle from the base of a male cone, above the entry of the traces of the basal bracts and their axillary buds. A series of inversely orientated bundles are seen.

(Dia. IV). At the stage of entry of the bundles of the two basal bracts and their axillary branches, the main series of bundles is more or less connected together into a ring, on the outside of which an increased number of inversely orientated bundles is present. One or two amphivasal bundles are also generally found inside the ring. This ring is broken up by the entry of the lateral bundles, and a very much folded mass of vascular tissue is then formed (see Dia. VII B).

Owing to the rapid succession of changes which take place at the origin of the bract bundles and those supplying the axillary buds or branches, it is extremely difficult to trace the exact sequence of events. In one case investigated the two

* WORSDELL (1901, p. 768–772) regards these, and possibly the whole pith, as representing tissue which primitively formed part of the xylem; the gradual transition referred to above is a fact which certainly supports his suggestion. (See also PEARSON, 1909.)

† Cf. *Cycadella* trunk, WIELAND, p. 66, fig. 35.

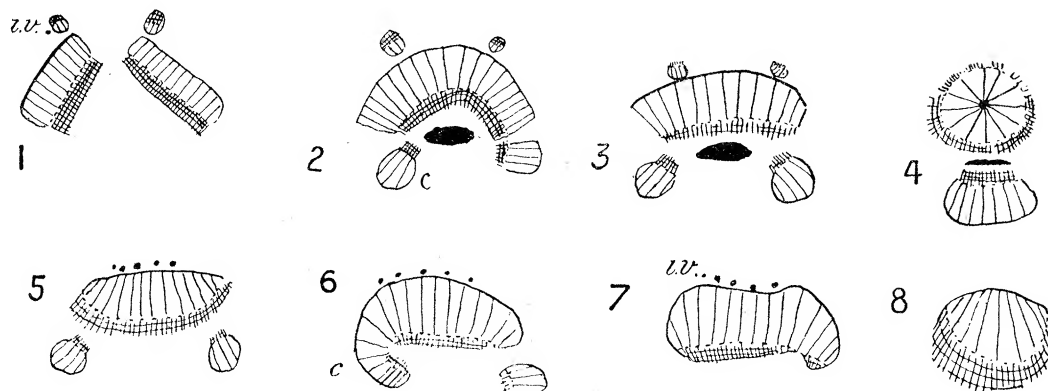
‡ The term “inversely concentric” is here used to describe concentric bundles in which the xylem occurs external to the phloem.

§ Cf. Amphivasal bundles of Monocots (*Dracena*), etc.

|| See WORSDELL; RANALES, 1908.

bract bundles each took their origin from two bundles of the stele; in all other cases they each appeared to be formed from a single bundle, as is the case with the two bundles supplying each of the cone bracts. The traces of the axillary buds or branches are complex in origin;* in the examples which I have examined, the axis of the bud received in addition to the two main bundles, each of which had a double origin, numerous small traces, one or more from each of the axial bundles of the outer series on the side subtending the bud. A fuller description of the changes which occur on the entry of these bundles will be given in connection with the female inflorescence (pp. 201–205).

Parts of the broken up vascular mass form large bundles; other portions give rise to smaller and inversely orientated bundles. These are grouped on the inner side of the larger bundles, each group presenting the appearance of a normally concentric bundle.† (The tissue occupying the centre of such a group of bundles is composed of elements with lignified walls.)‡



DIA. V, 1–8, shows the changes which take place in a single bundle when followed from above downwards.

At 1 two portions of the folded mass of vascular tissue described at the top of the peduncle are illustrated. A group of bundles is formed from these (2, 3, 4, 5), and from them one normal bundle is finally derived.

Radiating lines, phloem. Crossed lines, xylem. Blackened portion, centripetal xylem. *i.v.*, inversely orientated bundle. *c*, small bundles which fuse with main bundles.

Two of the largest of the main bundles were inversely concentric, and could be definitely traced to the fusion of a group of bundles entering from two lateral axes.

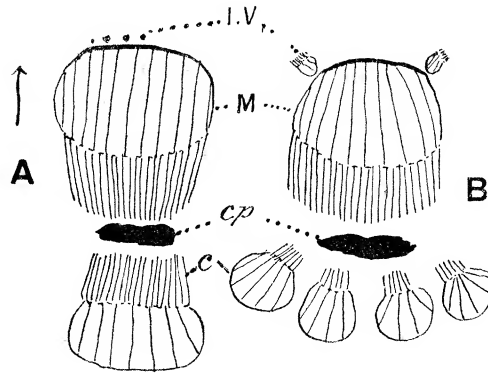
The inversely orientated elements present on the outer edge of the folded ring are still found on the outside of the larger bundles (Dia. V, *i.v.*); these persist almost throughout the portion of the axis examined (about 1 inch in length). Most of them gradually die away, but a few become connected with the xylem and phloem

* STRASBURGER, 1872, p. 144.

† Figured by STRASBURGER and by WORSDELL, 1901, p. 768.

‡ Compare centripetal xylem in peduncles of Cycadaceæ, SCOTT, 1897, pp. 403–404, 413–418, fig. 2, Plate 20.

of the main bundle. The smaller bundles formed from the folds of the ring mostly fuse one by one with each other, and finally with the sides of the main bundle (Dias. V and VI). During this process a normally concentric structure is often attained by the closing of the phloem round the xylem.*



DIA. VI, A-B, illustrates two bundles from the outer ring in the ultimate portion of an inflorescence axis bearing male cones.

M, main bundle. Other letters as above.

Three of the smaller bundles were found to end freely in a downward direction, and in one case a fairly large bundle ended freely upwards.

Diagram VIIA is taken from the level at which the normal peduncular structure is attained. Just below this stage a large inversely orientated bundle appeared. This was a new formation, and was not connected with the inversely orientated elements found higher up, but was probably continuous with the inversely orientated bundles formed at the next fork of the peduncle below. Occasional branching and fusion take place among the main bundles at all levels.

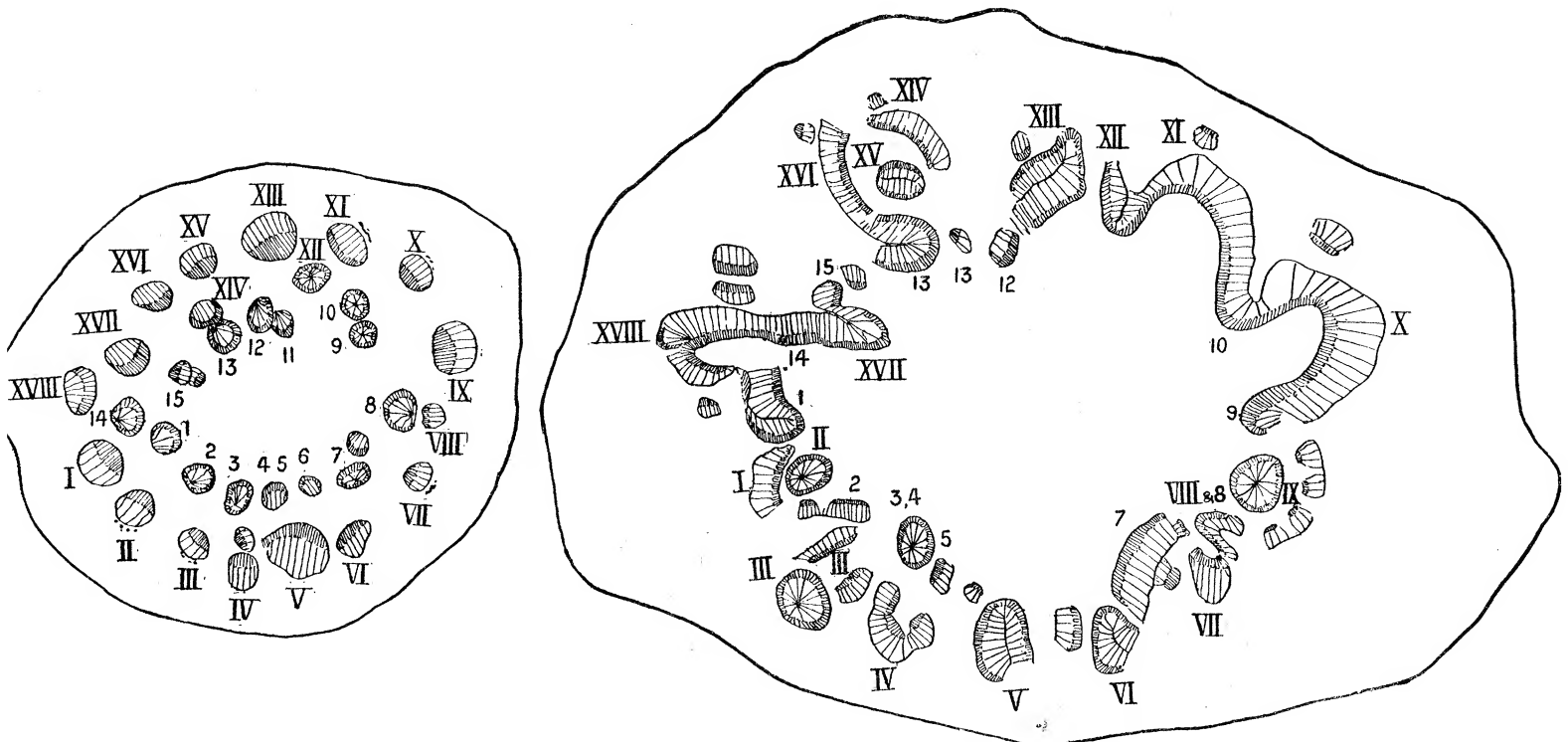
It may be of some interest to compare these diagrams with sections obtained from such stems of the *Medulloseæ*† as *Colpoxylon*. The waved outline of the steles in this genus and their occasional anastomoses are points of comparison with the bundles in the *Welwitschia* peduncle. On the other hand, the orientation of xylem and phloem in the two forms is, of course, different.

E. *The Female Flower.*

Each female flower is borne in the axil of one of the upper cone bracts, and consists of a short axis terminated by a single ovule which is enclosed in a winged outer covering, generally known as the perigone, and an inner covering, universally regarded as an integument. In a longitudinal section of a young or abortive ovule

* Cf. SCOTT, 1897, p. 407.

† RENAULT, 1896, *Colpoxylon*, Plate 67, figs. 1 and 2; WEBER and STERZEL, 1896, fig. 11, p. 35, etc.



DIA. VIIA.

DIA. VIIB.

Dias. VIIA and VIIB illustrate two sections of the ultimate portion of an inflorescence bearing male cones. A was cut about 1 inch below B, and was very near the base of the portion examined; B is taken at a level just below the entry of the traces from a pair of bracts, and the cones borne in their axils.

A. Most of the inner whorl of bundles are amphivasal at this level. A very few inversely orientated elements are present in connection with some of the bundles of the outer ring (III, VII, X, XI). Bundle 15 has only just appeared, and ends freely in a downward direction; 4, 5, the fusion product of two separate bundles, 4 and 5; 7 has just broken up into two.

B. At this level many additional small bundles have been formed by the folding of the cambium of the bundles in A. A little higher still, many of these bundles join up to form portions of a waved ring. Bundle 6, seen in A, has ended blindly and is not seen in B. Numerous inversely orientated bundles are now present.

(Lines wide apart, phloem; lines close together, xylem.)

(such as that represented in Dia. VIII, taken from the apex of a female cone, in which region the flowers seldom become mature),* several interesting points are to be noted. The stalk of the flower is comparatively long, and the length of the nucellus is small in comparison with that of the two coverings. The inner surface of the inner covering is strongly cuticularised for a considerable portion of its length (Dia. VIII, *M*).†

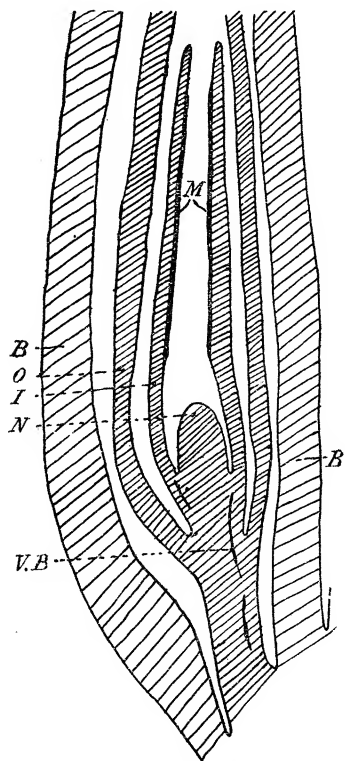
In older stages, it is seen that much intercalary growth takes place: the embryo-sac extends upwards from the level of the origin of the outer covering for some

* PEARSON, 1909, p. 333.

† Cf. STOPES (*Encephalartos*), 1904, p. 476; and LANG, 1900 (*Stangeria*), p. 286; and LIGNIER (*Bennettites morieri*), 1894, pp. 45-46, Plate 3, figs. 31 and 32.

distance above the insertion of the inner covering (Dia. XVIII); the two points being now at a considerable distance from each other.

In none of the stages which I have been able to examine is the seed fully ripe; consequently most of the structures which I have to describe are immature. In



DIA. VIII.—Abortive Female Flower in Longitudinal Section, seen *in situ* between two bracts (B).

O, outer integument; I, inner integument; N, nucellus; M, micropylar tube with cuticularised lining; V.B., vascular bundle.

particular, there was much difficulty involved in the investigation of the course of the vascular bundles, owing to their xylem being not yet lignified: in fact, many of them consist only of thin-walled cells arranged in radial rows. The following description applies to the oldest stages examined.

The *outer covering* is composed of a thicker portion enclosing the ovule, and two membranous wings (fig. 6, Plate 17).

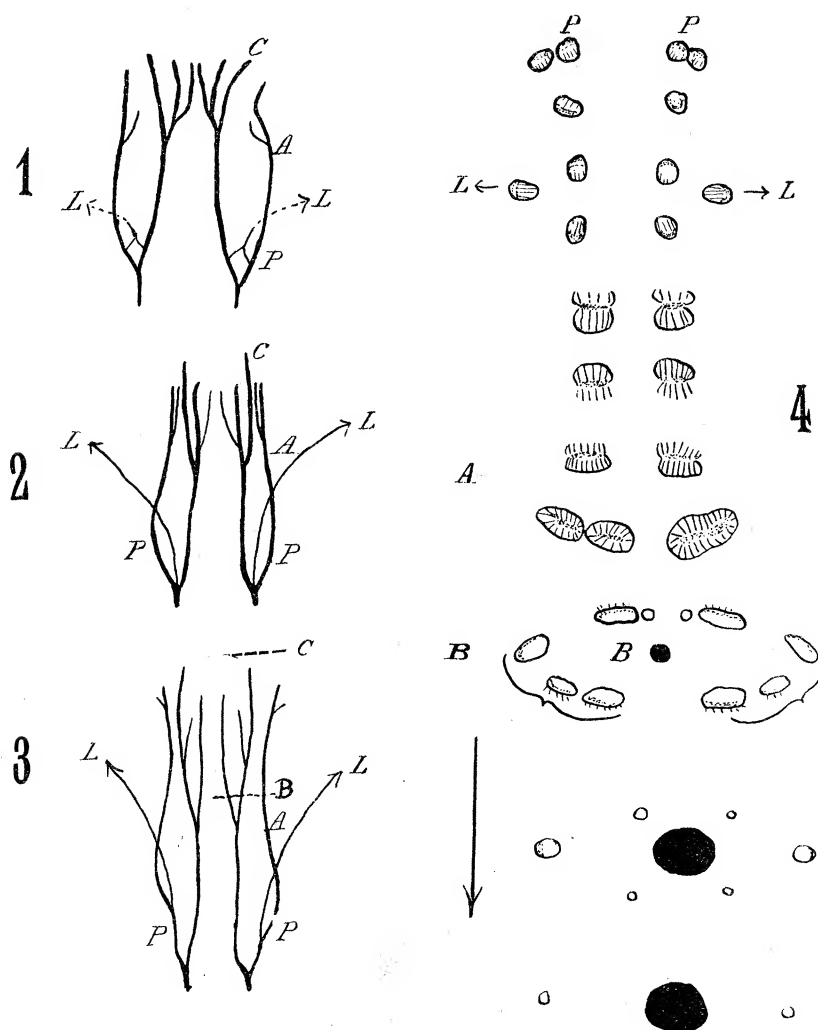
The thicker portion consists of several layers of isodiametric cells with thick walls, interspersed with groups of fibres, and bounded on the outer side by a thick-walled, small-celled, and on the inner by a thin-walled, large-celled epidermis. A median wedge of thin-walled tissue projects into each wing, but the wing itself is made up of numerous fibrous cells bounded by an epidermis. These pursue a somewhat sinuous course in the same section, some being cut transversely, others longitudinally (fig. 11, Plate 17); they are thick-walled, but unlignified, and resemble the fibres so often referred to in the descriptions of other parts of the plant. Two bundles run up the wings; in the oldest stages in my material the xylem

of these bundles is still unlignified, though the phloem is well developed. The elements are all arranged in radial rows and the bundles are endarch.

The *inner covering* is made up of from two to three layers of narrow, elongated, thick-walled cells. It extends above the tip of the nucellus forming the micropylar tube (fig. 6, Plate 17); the walls of the inner epidermis in the upper two-thirds of the tube become greatly thickened and cuticularised (see fig. 10, Plate 17).

The female flower stalk receives two *bundles*, whose course through the cortex of the rachis is similar to that in the male cone described above. The course of the two bundles in the flower axis varies slightly in different cases. The normal arrangement (Dia. IX, 1) appears to be as follows: four bundles are formed by the forking of the two main bundles, then each of these four bundles gives rise to a small trace. These

traces then fuse in pairs in the plane which corresponds to the principal plane of the ovule, that is to say, the fusion takes place between one trace from the anterior and



DIA. IX.—Course of Bundles in Axis of Female Flower.

1. Normal case, in which the bundles of the outer covering have a double origin.
2. Case in which two main bundles branch into three equal parts. (1 and 2 are built up from series of transverse sections.)
3. Case in which the two bundles of the outer covering arise from the two posterior bundles only. (Compare with Dia. II of male flower.)
4. Series of transverse sections from which 3 is built up.

N.B.—In all cases most of the perinucellary ring is derived from the two anterior bundles.

A, level of origin of outer integument; B, level of base of embryo sac; C, level of origin of inner integument; L, L, two bundles which supply outer integument; P, P, posterior bundles.

(Dotted area, phloem; radiating lines, xylem; black area, embryo-sac. Arrow points away from main axis.)

one from the posterior side of the axis. The two fusion bundles, which are thus of double origin, supply the outer covering of the ovule. It is probable that all cases

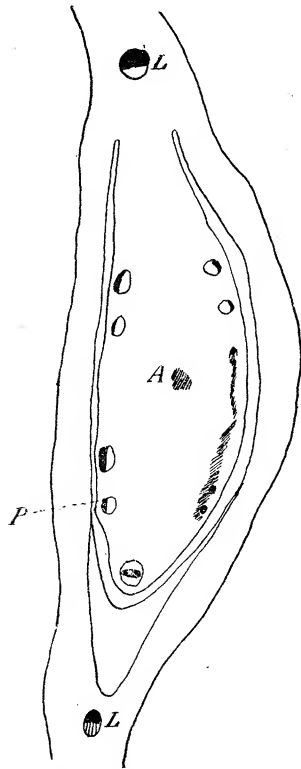
are referable to this general arrangement, though slight differences occur, which are to be attributed to a shortening of the normal process. Sometimes each of the main bundles forks once, and then the anterior bundles move away, while the posterior pair fork again (Dia. IX, 3 and 4). In some cases* the two main bundles divide at once, each into three portions (Dia. IX, 2). Occasionally the two bundles behave differently from each other. In any event, there are formed six bundles in the flower axis. After some considerable interval, the two median bundles move out into the

outer covering of the ovule; and, without further change, they pursue a straight course up the wings of this organ.

In the very young cone, the remaining four bundles run straight up the base of the ovule to the level of the insertion of the integument, but they do not appear to branch. In the older stages they branched considerably and somewhat irregularly, and it is possible that, in a fully mature state, they may form a more complex network. The first branching takes place at the level of the origin of the outer covering.

It is generally found that the posterior bundles branch less freely than the anterior ones.† Sometimes the posterior pair forked, and gave rise to two or more small bundles, or, in other cases, they did not branch again up to the level at which they died away. In most cases the anterior pair branched first once, giving rise to two lateral bundles, which moved into the regions of the principal plane of the ovule, and later forked again. In these cases eight main bundles were thus found running up the base of the ovule. Often several of the bundles fuse, giving rise to an elongated mass of meristematic tissue. Sometimes two of the main bundles give off small traces on their proximal side, and the pair thus formed fuse, as was seen in the male flower axis.

The two lateral bundles, those in the principal plane of the ovule, generally persist the longest. The other bundles extend nearly to the same level, and some of them generally give off a weak branch near the end of their course. This "perinucllary ring" of bundles dies out just at the level of the insertion of the inner covering of the ovule; no case of any bundles running into this



DIA. X.—Transverse Section, slightly oblique, of Female Flower.

L, bundles supplying outer integument; P, perinucllary ring of bundles; black portion, phloem; A, base of embryo sac. $\times 36$.

* STRASBURGER, 1872, p. 99; and 1879, p. 109.

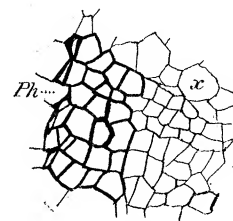
† As in Cycads, where the bundles which give rise to the integumental bundles branch less freely than the others, STOPES, 1904, etc.

organ were here found, but the whole system is clearly outside the region of the nucellus, if that region be defined by an arbitrary prolongation of the line of separation from the "integument." The system thus appears to belong to the integument, and not to the nucellus; this point will again be referred to later.

All the bundles at the base of the flower are collateral and endarch, but in some cases both they, and many of the bundles derived from them, become inversely concentric, and rows of thin-walled cells, which represent immature xylem, are found on the outer as well as the inner face of the phloem (Dia. IX, 4). All the elements are arranged in radial rows. In the oldest cases a few of the innermost elements were lignified, showing the bundles to be endarch.

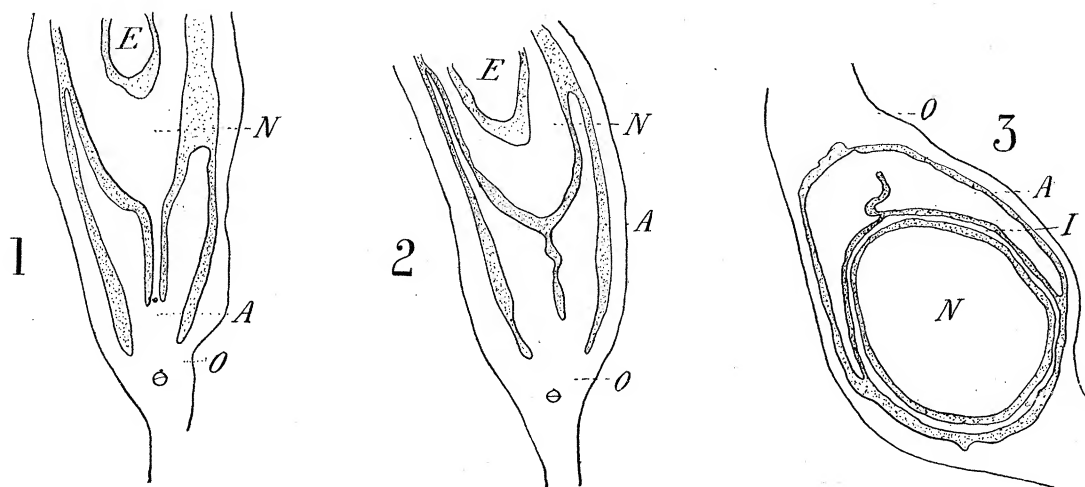
In the oldest cone examined an abnormal case was seen, in which the wing of the outer covering of the female flower was curiously lobed or ribbed on the surface towards the cone axis (fig. 11, Plate 17). The ribbing was quite irregular and was far more prominent in one wing than in the other. The phenomenon was seen to a small extent in two other cases.

Diagram XII illustrates a more interesting abnormality, in which a structure is present which is probably to be regarded as a further modification of this folding of the outer covering of the ovule. A flap was formed at the base of this ovule,



DIA. XI.—Showing Single Bundle. $\times 116$.

The xylem portion (*x*) of the bundle is entirely unlignified, but the phloem portion (*Ph.*) is thick-walled.



DIA. XII.—Series of Transverse Sections of an Abnormal Female Flower.

1. Abnormal outgrowth connected with outer covering. Taken at base of ovule, where outer covering is still connected with nucellus.
2. Abnormal outgrowth still connected with outer covering. From a higher level, at which outer covering is free.
3. Freely projecting portion of outgrowth. From upper portion of ovule, inner integument being now also free from nucellus.

E, embryo sac; *N*, nucellus; *I*, inner covering; *O*, outer covering; *A*, abnormal outgrowth or flap.

continuous by its abaxial surface with one side of the outer covering, and extending half way round the nucellus. No corresponding outgrowth occurred on the other side. Higher up, the flap became free from the outer covering and its tip projected upwards to about the level of the tip of the nucellus.

F. *The Axis of the Female Cone.*

The axis of the female cone is chiefly made up of parenchymatous tissue with rather well-developed intercellular spaces; it is bounded by a small-celled, slightly cuticularised epidermis. A large number of mucilage canals are found towards its periphery and are continuous with those of the bracts. The endarch collateral bundles are arranged in a single whorl, composed of four distinct crescent-shaped groups, with from six to three bundles in each and usually some additional bundles which occur in groups of two or three between the projecting ends of adjacent arcs. Associated with the main bundles are found from time to time smaller ones of variable destination. Some of the larger bundles are inversely concentric (fig. 12, Plate 17); their concentric structure is produced by the folding back of the normal cambium outwards, inversely orientated elements being then laid down by the external portion of the cambium. The number of these inversely concentric bundles increases towards the base of the cone, and at the extreme base a few of these also occur within the normal whorl of bundles. The course of the vascular bundles is more complicated than in the male cone axis, though referable to the same plan. Two bundles supply each bract, usually formed each by the forking of one of the corner bundles of one crescent-shaped group; and they pass straight out into the bract.

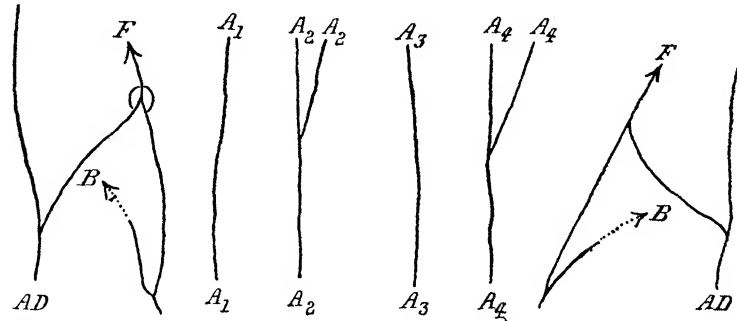
The bundles supplying each axillary flower are also two in number and as in the male cone both members of a pair have usually a double origin. Normally one-half of the bundle arises from the corner bundle of the crescent, from which also the bract bundle arose, and the second half arises from one of the small bundles which are found lying between the horns of two adjacent crescents; or, when such small bundles are lacking, it arises from the corner bundle of the next crescent. The two double bundles thus formed pass out into the stalk of the female flower and on their way pursue a course through the cortex similar to that described above in the male flower bundles.

This simple method of origin is not universal. It is illustrated by Diagram XIII, which is constructed from a series of cross-sections. Some of the slight variations are seen in Diagram XIV, but need not be described at length.

The formation of small bundles which end free is an interesting feature (Dia. XIV). These are often concentric. The bundles supplying the flower also often become concentric in their course through the flower axis (fig. 19, Plate 18). At *x* in Diagram XIV, the flower bundles branch, forming a concentric group, which opens out and becomes collateral as it passes into the axis of the female flower.

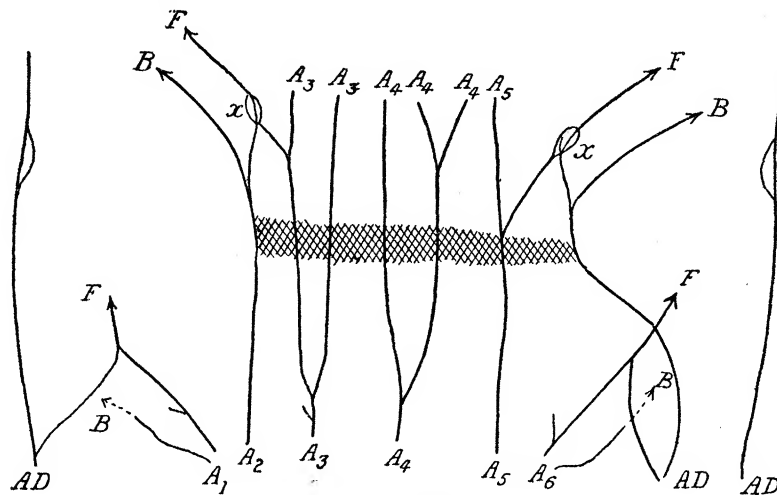
It will be seen from these diagrams that the main point of difference from the male cone depends on the weaker development and shorter course of the main bundles

here, branching being therefore more frequent and more variable. As in the male cone, none of the bundles are cauline but at some level each takes part in the formation of bract and flower traces.



DIA. XIII.—Illustrates a Part of the Course of the Bundles (A, A_4), forming one of the Crescent-like Groups.

(B , bundle supplying bract; F , bundle supplying flower; AD , adjoining bundle.) Here B and part of F originate from a corner bundle, which is completely used up in their formation. The other half of F arises from a trace supplied by a small adjoining bundle. The number of bundles in the crescent group is restored by the branching of A_2 and A_4 .



DIA. XIV.

(Letters as before; cross-hatching, anastomosis of bundles.) The lower pair of bract and flower traces probably originates as in Dia. XIII, A_1 and A_6 being used up in their formation. A_3 and A_4 then branch to restore the original number of bundles in the group. In the formation of the right-hand member of the upper pair of flower traces, the corner bundle (A_5) is not used up, but part of it runs on afterwards in the cone-axis; the bract bundle arises in this case from the adjoining bundle (AD), which also contributes to the flower bundle, and is thus used up. On the left the bract trace arises normally from one of the main bundles of the crescent (A_2), but the flower trace is composed of the remaining portion of A_2 and a small trace from A_3 .

G. Naked Axis of Female Inflorescence (Female Peduncle).*

The *general structure* of the axis of the female inflorescence is similar to that of the male. The pith is thin-walled and unligified, except towards the base of the old

* STRASBURGER, 1872, p. 99, and figs. 43, 44, Taf. 19.

peduncle, where it consists entirely of cells with lignified and reticulately pitted walls similar to those composing the pith throughout the male inflorescence.

The course of the bundles at the points of branching is found to be extremely complicated; it has been followed more minutely than in the male peduncle, but the two are similar in all essentials. There are many variations, but one case only need be fully described.

The peduncle bore at its apex a terminal cone with two aborted lateral buds in the axils of bracts. At the base of the cone were two bracts with acute apices, in the axils of which were also minute aborted buds. The normal structure of the cone-axis becomes disturbed a little above the level of these bracts, and the bundles are irregularly arranged in a ring, some of them taking up their position in the cortex outside the ring. Many of the bundles have become inversely concentric; there are also numerous inversely orientated strands on the outer edge of the bundles and a number of lignified elements have been developed on the inner edge, in the position of centripetal xylem.

At least six bundles enter from each of the two aborted buds at the base of the cone. Some of these break up to form small groups of bundles, the bundles of each group being arranged with their xylems turned towards each other, forming together a large normally concentric bundle;* this transitory group is very soon split up, and all the bundles entering from the bud, with some bundles mentioned above as already present in the cortex, form a definite outer series in the cortex of the axis. Two of the largest of these bundles, laterally placed, now fuse each with one of the bundles of the inner ring, a smaller portion of them becoming at the same time connected with one or more of the other bundles. Just below this level, two bundles from the bract in the axil of which the bud was placed enter and fuse with the same two bundles in the stele which have already received the larger portion of the two lateral bundles of the bud. At about the level of entry of the bract traces, the remaining bundles which enter from the bud form a more or less definite row, which at one stage becomes connected into one elongated mass, orientated inversely to the bundles of the main inner stele. Later this mass breaks up again, and some of the bundles fuse with those of the inner ring, but the greater number remain separate in the cortex, and form, after various contortions, a very large inversely concentric bundle; this bundle has a very striking appearance and is continued right down into the peduncle without anastomosis with the other bundles, except where it is disturbed by the entry of a strand on either side from the next two bud traces.

Comparison with other cases shows that such a large cortical bundle is often similarly formed by some of the bundles entering from a bud; in one case this bundle was normally concentric. These bundles are always formed on the longer sides of the oval axis of the stele. From the bud on the opposite side to that described above three inversely concentric bundles were formed.

* WORSDELL, 1902, pp. 767-768.

The bundles of the inner ring are now mostly collected into two lateral series, and the traces from the lowest pair of lateral buds next enter, behaving in a manner essentially similar to those of the upper pair. The two main bundles from a bud, and the two bract bundles, fuse with the ends of the two lateral series in the stele; most of the intermediate bundles, with some of the outer cortical bundles of the axis, form an elongated mass of tissue, which after the entry of the two bract bundles connects up the two lateral series of bundles in the stele, forming again the inner ring; a few of the small bundles remain in the cortex at the ends of the oval stele.

In cases of branching, where the lateral axes are fully developed, the processes involved in the entry of the lateral traces into the stele are very similar to those described for the bundles of the aborted buds, but the disturbance created in the stele is still greater. It can, however, always be seen that the two largest of the numerous bundles, those probably representing the original supply of the lateral axis, originate from the inner series of bundles.

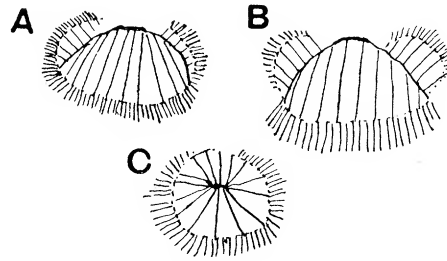
A definite convoluted ring of vascular tissue, such as is found at the points of branching in the male inflorescence axis, does not commonly occur in the female. The variation in arrangement is probably dependent on the shorter or longer intervals over which the disturbance extends. In the cases in which a waved ring is formed, it speedily breaks up.

Below the points of branching the bundles become arranged in two whorls, the inner more or less amphivasal, the outer composed of large amphivasal or collateral bundles, round which smaller ones are grouped. The groups of bundles have the same concentric arrangement as those on the periphery of the male axis. The smaller bundles of each group may fuse together, so that each group forms a pair facing each other,* or they may remain for some time separate, but finally the inner portion of each group fuses with the outer (see Dia. V, p. 193), moving round so that its xylem and phloem become applied to the corresponding tissues of the main bundle. Associated also with many of the bundles of both rings is a more or less complete ring of smaller inversely orientated bundles, some of which gradually fuse with these, while others end freely or (chiefly on the centripetal side of the main bundles) become represented only by a few scattered xylem elements. These latter are generally rather short, with reticulately pitted walls, and wider than the elements of the centrifugal xylem of the main bundle, recalling the transfusion tissue sheath of the leaf bundle.

Between the points of branching the bundles run straight down with very few anastomoses. They are more or less definitely arranged in two whorls; groups of cells with lignified walls are present on the centripetal side of the xylem, and also surround the mucilage cavities found in the upper portion of the axis.

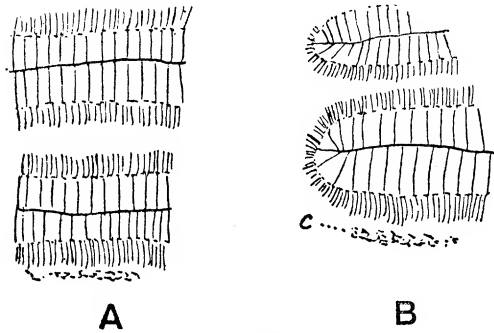
A number of quite large inversely orientated bundles occur at intervals on the

* Cf. Dia. VI, A and B, of male axis, p. 194.



DIA. XV.—A Bundle from the ultimate Branch of a Female Inflorescence.

At A, two smaller bundles are seen to be produced by the folding of the cambium; at B these increase in size; at C the main bundle becomes amphivased, and the two smaller ones are again absorbed.

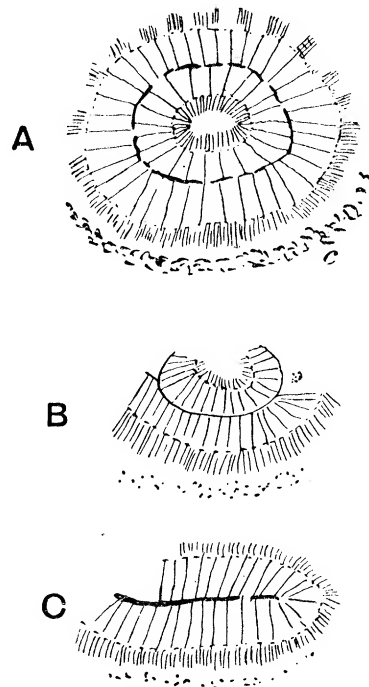


DIA. XVI.

A shows four parallel bands of xylem and phloem which were formed by the folding of the cambium of one of the main bundles from the outer ring in the basal region of a peduncle bearing female cones.

B shows one of the stages in the folding. A large bundle with an inverse band of tissue is present, and on its outer side is a second similar and smaller bundle.

(c, cells with lignified walls in a centripetal position.)



DIA. XVII.—Bundle from Basal Region of Female Inflorescence, seen at different levels.

A, level at which a small concentric bundle appears to be surrounded by a band of xylem and phloem. (c, cells with lignified walls centripetal to the bundle.)

B, lower level, the outer band of vascular tissue has formed a normal collateral bundle, the inner concentric bundle is also becoming collateral, though inverse to the larger bundle.

C, lower still. The cambium of the smaller bundle is now continuous with that of the larger; at a lower level the two probably give rise to a normal collateral bundle.

outer side of the main bundles, and are formed anew, generally in pairs, from a main bundle (Dia. XV); sometimes they become detached from the main bundle, but later fuse with it again.*

It is very rare for the main bundles to end freely. One fairly large bundle traced from below was seen to end free beneath a mucilage cavity.

At the extreme base of the inflorescence axis, just above its origin from the stem, a very large number of bundles are found. There is an inner ring of fairly regular amphivasal bundles, and an outer series, two or three deep, of scattered collateral bundles, which are irregularly folded in various ways and give rise to small inversely orientated bundles and even to normally concentric bundles (Dia. XVII, p. 204). In one case four bands of phloem and xylem were formed in this way by folding (Dia. XVI, p. 204), an arrangement which recalls the rings of secondary thickening found in some Cycads.†

SECTION III.—MORPHOLOGY OF THE INFLORESCENCES OF *Welwitschia*.

A. *Branching of the Inflorescences.*

Their profuse branching is one of the most striking characters of the inflorescences of both sexes in *Welwitschia*. As far as I know, such dichasial cymes are not to be paralleled among the recent Gymnosperms outside the Gnetales. Although the stems of recent Cycads are now known to branch more frequently than was formerly supposed,‡ there is nothing in that family at all comparable with the dichasial cymes of *Welwitschia*.

Among the fossil Cycadoideæ, however, one of the most remarkable genera, *Williamsonia angustifolia* (*Anomozamites minor*),§ was branched dichasially. At each point of branching the main stem seems to have ended in a bud surrounded by a tuft of leaves, or in a *Williamsonia* strobilus, also enclosed in sterile leaves. This arrangement presents various points of striking resemblance to *Welwitschia*, where at each place at which the dichasial cyme branches two sterile leaves occur, in the axils of which the lateral branches arise, while in the fork is commonly found a cone with, in the female, many sterile bracts at its base. This comparison may be a mere analogy, but the similarity in position of the *Williamsonia* strobilus and the *Welwitschia* cone is, at any rate, remarkable.

* Possibly these are to be compared with the strands remarked on by SCOTT in Cycadean peduncles (SCOTT, 1897, p. 408). In the Cycads these strands end freely in the cortex, and SCOTT suggests that they may represent a vestigial leaf-trace system. If these bundles in *Welwitschia* are of similar nature, they may represent a leaf-trace system still further reduced.

† See WORSDELL, 1906, etc. In this connection, the concentric rings of secondary thickening in *Gnetum scandens* are also of interest.

‡ WORSDELL, 1906, p. 130 ff.

§ NATHORST, 1888, pp. 359–365; WIELAND, pp. 38 and 41, fig. 12.

B. *Comparison of the Male and Female Inflorescences.*

The facts bearing on the comparative morphology of the inflorescences, cones and flowers have been summarised by PEARSON,* and in his latest paper† he tabulates the various views of other observers.

From his recent detailed description of the inflorescences and from the shorter account given in this paper, it would at first sight appear that as the inflorescences bearing the male and female cones are dichasial cymes of essentially similar structure, both they and the cones of the two sexes are strictly comparable.

The remarkable discovery of megaspores in the axis of the female cone has, however, led PEARSON‡ to consider the possibility of regarding it as morphologically different from the male cone. He suggests that the *female* dichasium is derived by proliferation from the cone, and that the lateral cones directly replace flowers, so that each of the lateral female cones is comparable with a single male flower. Thus the axes of the lateral female cones are regarded as proliferated nucelli, and in this way the occurrence of anomalous megaspores is accounted for. The occasional examples of arrested inflorescences bearing a single female cone§ may possibly be regarded as supporting PEARSON's view.

In working out his hypothesis he compares the various kinds of bracts borne by the cones of both inflorescences. He compares the "acute" basal sterile bracts, occurring at the base of each female cone and at the points of branching, with the non-vascular bracts at the base of the separate axillary male flowers, while he regards the rest of the bracts of the female cone, both sterile and fertile, as derived from the tissues of the proliferated nucellus.

The mature structure of the cone bracts had not then been fully investigated; the facts now described|| lend no support whatever to such a theory. All the adult bracts of both male and female cones resemble in essentials the sterile basal bracts; it is therefore difficult to regard any of them as morphologically distinct from the others, and still more difficult to draw a particular comparison between the non-vascular bracts of the male flower and the basal bracts of the female cone.

Moreover, if proliferation explains the dichasium in one case, there seems no reason why it should not also explain it in the other. Anomalous megaspores would be unlikely to occur in the axis of the male cone where the ovules are themselves abortive,¶

* PEARSON, 1906, pp. 277 and 284.

† PEARSON, 1909, Tables I and II, pp. 336 and 338.

‡ PEARSON, 1909, figs. 1, 1a, b, c, Plate 1, and pp. 334 ff.

§ PEARSON, 1909, p. 332, and *ante*, p. 184.

|| *Ante*, pp. 184-186. It has been shown that the structure of all the cone bracts, and also of some regions of the peduncles, is similar, if examined at a similar age. The comparison on p. 340 of Prof. PEARSON's paper is thus invalidated, though the conclusion reached, "that the vascular structure of these organs does not support the homologies suggested" by him, is confirmed.

¶ PEARSON, 1909, p. 335.

and their presence in the female cone axis should only be used as an argument for proliferation in general; it may lend support to the theory that the ovule is cauline, not foliar as the stamen appears to be, but even on that point this class of evidence seems to me to be questionable, and the cone homologies are not affected. Indeed it appears to me that the occurrence of the anomalous megaspores is a character so aberrant that it is dangerous to base on it any argument concerning morphology.

All the other facts disclosed in this investigation have also led me to regard the separate axillary male and female flowers as homologous. Firstly, the method of vascular supply of the peduncles, cone axes and bracts in both sexes, also of the axes of both male and female flowers, is essentially similar; such close similarity would hardly be expected if the structures were not homologous. Secondly, the vascular structure of the flowers themselves is clearly comparable; the aborted ovule of the male flower has a double system of vascular bundles derived from the axis of the flower in exactly the same way as those supplying the fertile ovule of the female flower.

C. *Comparison of the Individual Male and Female Flowers.*

It appears to me that the most reasonable view of the morphology of the female flower in *Welwitschia* is that which regards it as consisting of a nucellus with two integuments, the outer winged and free to the base, the inner prolonged into a tube and only free from the nucellus at the apex. The main reason for regarding the outer covering as an integument is the position of the embryo-sac, which extends downwards to the level of the outer covering, and thus occupies a position essentially comparable with the position of the embryo-sac relatively to the outer integument in *Lagenostoma*, and other seeds. Comparative evidence derived from fossil and recent seeds will be found considerably to strengthen this view, and it will be assumed in the comparison of the male and female flowers which follows.

It is impossible to be certain whether the single integument of the aborted ovule of the male flower represents the outer or inner integument of the female. From its general configuration and its absence of vascular supply it would appear to be comparable with the inner integument; in its development, on the other hand, it resembles the outer, for it arises from two separate primordia and not from a single ring as does the rudiment of the inner integument.* The absence of even a reduced remnant of an embryo-sac also suggests that what appears to be the nucellus really represents an undeveloped mass of tissue not differentiated into nucellus and inner integument. This seems the more probable since the two bundles found running up into the outer integument of the fertile ovule are represented† by two well-developed

* MACNAB, 1872, p. 509.

† *Ante*, pp. 188-190.

bundles which die out at the base of the single covering of the abortive ovule. The difference in general configuration between this single covering and the outer integument of the female flower is readily explicable as depending on its different relations with the surrounding structures, the one being equally enclosed on all sides by the fused staminal filaments, the other being flattened and appressed in the axil of the bract.

An interesting parallel to this absence of one of the coverings in the case of the sterile ovule is afforded by *Gnetum*. In that plant STRASBURGER has described* (i) fertile female flowers of the ovulate spikes with three coverings, and (ii) sterile female flowers of the staminate spikes with two coverings; LOTSY† also discovered‡ occasional specimens of fertile female flowers in the staminate spikes, and these have always three coverings.

There is nothing in the female flower to correspond with the ring of stamens in the male, and there does not seem any *à priori* necessity that the female flower was ever primitively hermaphrodite. The non-vascular bracts at the base of the male flower are also additional structures and are difficult to homologise; there is no evidence to show that they ever had a vascular supply or have been derived from the ordinary bracts; it is just possible that they may come to be regarded as sterilised sporophylls,‡ or that they may be more properly compared with accessory structures such as the hairs at the base of the sorus in the Schizeaceæ.§ Whether they are to be placed in the same category as the Angiospermous perianth must as yet remain undecided.

D. *Comparison between the Ovules of Welwitschia and some other Gymnosperms.*

The view which regards the fertile ovule in *Welwitschia* as consisting of a nucellus with two integuments receives considerable support from a comparison with such a seed as *Lagenostoma*. The value of this comparison is increased by the ease with which the structure of other seeds can be interpreted as modifications of the same ground plan.

The vascular supply of the ovule in *Welwitschia* appears to be entirely integumental. Two bundles run up to the apex of the outer integument, while those traversing the perinucellary zone die out at the level at which the inner integument becomes free from the nucellus. That these belong to the inner integument and not to the nucellus is rendered probable by their position, their course|| being entirely restricted to that part of the ovule which lies outside the region of the nucellus

* STRASBURGER, 1872, pp. 102-105; 1879, p. 101.

† LOTSY, 1899; COULTER and CHAMBERLAIN, p. 123.

‡ See WORSDELL on the perianth in Angiosperms, 'New Phyt.', 1903, and RENDLE, 'New Phyt.', 1903.

§ It is also possible that they may represent a rudimentary encasement such as that from which the outer integument of the ovule has been derived. (Cf. the rudimentary integument round the male sporangium in *Lepidocarpon*).

|| Pp. 197-199.

as it is defined by an arbitrary prolongation of the line separating the nucellus from the integument.* This suggestion receives confirmation from an examination of the seed of *Gnetum africanum*, where the inner perinucellary system *extends into the base of the inner integument*.†

(i) The cupule and inner integument of the radially symmetrical seed of *Lagenostoma*‡ are at first sight very different from the flattened “perigone” and tubular inner integument of *Welwitschia*.

There are, however, several points of striking resemblance between these two seeds. Both seeds have an outer integument free to the base from the nucellus, and similarly supplied with vascular bundles which run from base to apex; they have also an inner integument which is free only for a short distance at the apex, and has a vascular system, and in both seeds the position of the embryo-sac is essentially similar, extending downwards to the level of origin of the outer covering.

The main points of difference between the two seeds are probably associated with the evolution of siphonogamy; while the inner vascular system of *Lagenostoma* is persistent up to the apex of the nucellus, the second and inner series of bundles in *Welwitschia* does not run up into the free portion surrounding the nucellar beak.§ In *Welwitschia* the nucellar beak, present in both seeds, is much more elongated, and the embryo-sac extends upwards into the base of the nucellar beak, the whole arrangement being admirably adapted to the peculiar method of fertilisation.||

(ii) In the Cycads there is much evidence to suggest that the seed may be similarly interpreted, the integument being a double organ in which the original separate nature of the two integuments can now only be detected in the double system of vascular bundles. It was early noticed that the inner or “perinucellary” system of bundles does not lie in the plane of fusion of nucellus and integument, but that the bundles exhibit a centrifugal tendency.¶ The hypothesis that this system of bundles in the Cycads belongs really to the inner integument** was tentatively suggested by both MATTE†† and WORSDELL‡‡, and has recently been more clearly established, since it has been shown§§ that they sometimes run up towards the apical portion of that organ beyond the level at which it becomes free from the nucellus.

* Cf. OLIVER, 1903, p. 458, and *Physostoma*, 1909, p. 85.

† THODAY, M. G. (SYKES, M. G.), Brit. Ass. Sheffield Meeting, 1910. A detailed account of this seed will appear later.

‡ OLIVER and SCOTT, 1904.

§ N.B.—In regard to this character, *Gnetum africanum* forms a link with *Lagenostoma*.

|| PEARSON, 1906 and 1909.

¶ See OLIVER, 1903, p. 458.

** The author was led quite independently to this hypothesis before becoming acquainted with the suggestions and evidence accumulated by Dr. STOPES.

†† MATTE, p. 168.

‡‡ WORSDELL, 1906, pp. 154–155.

§§ STOPES, 1904, pp. 439, 442, 468–470, fig. 37, p. 473.

Cycas, which has bilateral symmetry, is especially interesting for comparison with *Welwitschia*. The two bundles, supplying the outer covering of the one and the outer layer of the integument in the other, run in the principal plane of the ovule, while the inner ring of bundles in *Welwitschia* is comparable with that supplying the inner layer of the integument in *Cycas*; they are often even similarly derived, partly directly from the bundles of the flower axis and partly from the branching of those bundles which supply the outer covering.

(iii) Another Gymnospermous seed which is of considerable interest for comparison with both *Welwitschia* and *Cycas* is the Palæozoic seed *Cardiocarpus*,* which is by BRONGNIART referred to the Cordaitean group. It is bilaterally symmetrical and has a single distinct covering which in some Cordaitean seeds may ripen, dry, and bear wings like the outer covering in *Welwitschia*.† This covering is fused for some distance with the nucellus, and supplied with two vascular bundles, which run in the principal plane of the ovule to the tip of the covering. There is also an inner or perinucellary ring of bundles which terminates at the level at which the integument becomes free from the nucellus.‡

This single integument in *Cardiocarpus* has been compared with the inner integument of *Lagenostoma*, and the inner or perinucellary system has been regarded as belonging to the nucellus. RENAULT,§ however, found that in *C. angustodunensis* the inner system of bundles exhibits a centrifugal tendency and lies outside the province of the nucellus. It may be suggested that here, as in the Cycads, the integument is a double organ, to which the two outer bundles and this inner ring of bundles belong. The seed agrees with *Welwitschia* in that its inner ring of bundles is much reduced.

To sum up this comparison it thus appears to me that the seeds of *Lagenostoma*, *Welwitschia*, *Cardiocarpus*, and the Cycads are constructed on the same ground plan. Each of these seeds can be regarded as consisting of a nucellus with two integuments, the inner of which is never free from the nucellus except at the apex. In the first two forms the outer integument is free to the base, in the others it is fused with the inner integument. In no case is there any vascular supply to the nucellus or pollen-chamber, but a double system of vascular strands supplies the two integuments, and is seen in its most primitive condition in *Lagenostoma*. The outer ring of strands is always persistent up to the apex of the outer integument, but the inner system in the Cycads is only occasionally found running up beyond the level of freedom of the integument, while in the other seeds it always dies out at the base of the free portion.||

* BROGNIART, 1881; RENAULT, 1896; OLIVER, 1903.

† COULTER and CHAMBERLAIN, p. 141.

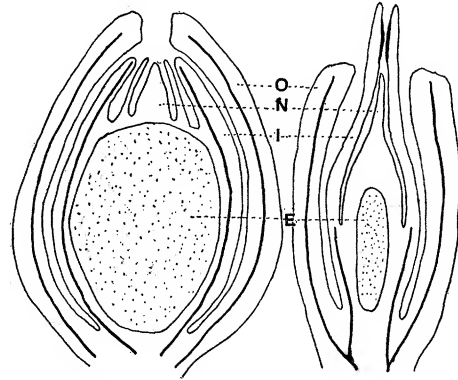
‡ OLIVER, 1903.

§ RENAULT, Part II, p. 385. See OLIVER, 1903, p. 458.

|| Contrast *Gnetum*, p. 209.

The outer integument of *Welwitschia* is thus comparable with the cupule of *Lagenostoma* and the outer layer of the integument in *Cardiocarpus* and the Cycads, while the inner integument is to be regarded as equivalent to the inner integument in *Lagenostoma* and the inner layer of the integument in the other forms.

One remarkable point in which the *Welwitschia* ovule differs from all others (except perhaps that of the Bennettitales)* lies in the extraordinary elongation of the nucellar apex. This elongated portion I regard as secondarily derived by the growth of the apex of both nucellus and integuments. That this region is capable of great elongation does not seem surprising; a small nucellar projection is present in many seeds, and LANG† has shown how in *Stangeria* it at first keeps pace with the integument in its growth. In *Stangeria* the superficial cells of the nucellar tips are thickened as they are both in *Welwitschia* and in *Cardiocarpus*‡; also as the integument projects and forms a narrow micropyle its margin becomes thickened, as it does also in a very striking manner in *Welwitschia* and in *Bennettites morieri*.§



DIA. XVIII.—A Diagrammatic Representation of the Ovules of *Welwitschia* and *Lagenostoma*.

O, outer integument (wings omitted); I, inner integument; N, nucellus; E, embryo-sac.

SECTION IV.—OTHER POINTS OF THEORETICAL INTEREST IN THE ANATOMY AND MORPHOLOGY OF *Welwitschia*.

A. Double Origin of the Bundles Supplying the Appendages.

In *Welwitschia*, the traces of cotyledons, young leaves, bracts, and flowers have a double origin from two separate bundles of the stele of the axis. Their origin thus differs from that of the double leaf-trace so characteristic of most Gymnosperms, which arises from a single bundle of the axis, and branches into two during its course through the cortex. Perhaps the origin of the double foliar bundle in *Ginkgo biloba*|| may be looked upon as intermediate in character; in that genus a single stelar bundle divides into two separate portions, which then run side by side for a short distance in the axial stele before passing out into the leaf.

The two bundles supplying the cotyledon in *Welwitschia* probably represent

* LIGNIER, 1894, Plate 11, fig. 28; WIELAND, p. 122, fig. 63.

† LANG, 1900, pp. 285–286, fig. 12, Plate 18.

‡ Cf. BRONGNIART, 1881, Plate 3, figs. 8 and 13.

§ LIGNIER, 1894, pp. 45–46, Plate 3, fig. 31.

|| SEWARD, A. C., and GOWAN, J., 1900, figs. 24–27, Plate 9. (Also cf. Cordaites, WILLIAMSON, 1877, Plate 9, pp. 44 and 46.)

a reduction from the four bundles supplying the cotyledon in the Cycads, etc.,* and may possibly be regarded as a stage towards the reduced vascular supply of the Angiospermous cotyledon, in which a relic of the paired bundles is still often traceable in the peculiar V-shaped bundle recorded by various observers.†

The double vascular supply of the "flowers" in *Welwitschia* is closely paralleled among the Cycads,‡ where the two bundles supplying the ovules often have a separate origin from two adjoining bundles of the axis; the arrangement in *Welwitschia* is, however, rendered still more complex by the fact that each of the two bundles here supplying the flower has itself a double origin. But the main course of the bundles in the cone-axis of the Cycads and *Welwitschia* is essentially similar; to take a concrete example, *Dioon edule* may be closely compared with *Welwitschia*. The axis of the cone of *Dioon*§ has several arcs of bundles together forming a regular whorl and the two ends of each arc provide the bundles supplying the ovules. In the median region of the cone the traces entering from the ovules are double, and they may unite with the same or with separate bundles of the crown. Similarly other genera of Cycads may be compared with *Welwitschia*. In *Ceratozamia*,|| *Zamia*,¶ and *Bowenia*** two bundles commonly enter from the scales and join two separate bundles in the axis.

B. Inversely Orientated and Concentric Bundles.

The presence of inversely orientated bundles, in connexion with the main bundles, at the base of the ovule of the female flower, at the base of the male and female cones, and at intervals throughout the male and female peduncles, is one of the most striking points in the anatomy of *Welwitschia*. Similar bundles have been recorded in the Cycads†† and in *Ginkgo*,‡‡ e.g. in the ovuliferous scales of *Cycas neocaledonica*,§§ and *Ceratozamia*,|||| in the peduncle of *Encephalartos*¶¶ and *Ceratozamia*,*** and in *Cycas circinalis*,††† etc.

* TANSLEY, A. G., and THOMAS, E., 1906; THOMAS, E., 1907, p. 84.

† SARGENT, E., 1908, pp. 162-164, etc. A theory suggesting the derivation of the V-shaped bundles of the Angiosperm cotyledon from the double leaf-trace of Gymnosperms, etc., has also been brought forward by Miss THOMAS, 1907.

‡ WORSDELL, 1898, p. 206; MATTE, H., fig. 159, Plate 10; fig. 184, Plate 12, etc.

§ MATTE, H., pp. 113-115.

|| *Ibid.*, pp. 123-124, fig. 174, Plate 11.

¶ *Ibid.*, p. 130, fig. 184, Plate 12.

** *Ibid.*, fig. 224, Plate 14.

†† WORSDELL, W. C., 1898, p. 213; WORSDELL, 1906, p. 145; and H. MATTE, Plates 10, 12, etc.

‡‡ SHAW, F., 1908, p. 87, fig. 16.

§§ MATTE, pp. 103-104.

|||| *Ibid.*, p. 118.

¶¶ *Ibid.*, figs. 223, 225.

*** SCOTT, D. H., 1897, p. 412.

††† WORSDELL, 1898, figs. 2, 4, Plate 17.

These inversely orientated bundles in the Cycads are strictly comparable with those of *Welwitschia*; they are similarly formed only of secondary elements and their special cambial zone is at some level in direct continuity with the cambial zone of the normal bundles, the margin of which is recurved.*

In the Cycads as in *Welwitschia* there are sometimes also found elongated bands of inversely orientated elements, forming with the normal ring a continuous mass of tissue with xylem both external and internal to the phloem;† in the posterior or inverted portion of the band no primary elements can be recognised.

The figure of the hypocotyl of *Cycas siamensis*‡ given by MATTE is remarkably like the structure of the *Welwitschia* inflorescence axis at the points of branching.

Occasional normal concentric bundles are found in the *Welwitschia* peduncle, and at the origin of the bundles supplying the female flower, the traces of the stamens are also regularly concentric. With the exception of the last named, which have already been compared§ with the bundles supplying the ovules in *Bennettites* all these formations are due to the approximation of small secondarily formed bundles to a main bundle; and the group finally fuses together to form a normally orientated bundle. MATTE|| and WORSDELL¶ conclude that such inverse and concentric bundles are reminiscences of the polystelic structure of the Medulloseæ.** The four concentric groups†† found in the hypocotyl of *Welwitschia* certainly recall this group, but there does not seem to me sufficient evidence for regarding polystely as primitive in the ancestry of *Welwitschia*. The great development and preponderance of secondary tissue which is such a feature of the Medulloseæ and of all the Cycadean alliance is remarkably striking in *Welwitschia*, where, indeed, the whole of the vascular tissues of the inflorescences, cones, and flowers appears to be derived from the divisions of a cambium. The series of inversely formed elements in *Welwitschia*, sometimes consisting of three to four bundles, back to back (Dia. XVI), also the successive rings of bundles formed in the hypocotyl, are strikingly suggestive of the extrafascicular rows of cambium in the stems of the Cycads. There can be little doubt that the close resemblances with both the Cycads and the Medulloseæ indicate some phylogenetic relationship between the three families.

* MATTE, p. 105.

† MATTE, H., p. 105, figs. 147-149, Plate 10 (at the base of the ovule in *Cycas*).

‡ *Ibid.*, p. 189, fig. 248, Plate 15.

§ Page 187, and WORSDELL, 1901, p. 767.

|| MATTE, p. 164.

¶ WORSDELL, 1901, pp. 770-771; and WORSDELL, 1906, p. 141.

** See also *ante*, p. 194.

†† BOWER, 1881; SYKES, M. G., 1910 (*in ed.*)

C. Centripetal Xylem and Transfusion Tissue.

The centripetally developed, isodiametric tracheides at the base of the cotyledonary bundles* may possibly represent the centripetal xylem of the Cycads, etc. Very little transfusion tissue is present in the cotyledon, even at the stage when the cotyledon is about to drop off, and even this is best developed on the phloem side of the bundle. There is therefore no possibility of tracing any continuity between this tissue and the centripetal xylem.

In the young leaves and bracts it also arises in the same position†; in the old leaves it forms a well defined ring in the pericyclic region of the bundle. Sometimes in the developing bundles of the bracts the transfusion tissue arises before the xylem is lignified, but always on the phloem side of the bundle. In the old bracts, isodiametric cells with lignified and pitted walls appear to arise from any parenchymatous cell, and this part of the transfusion tissue extends out for some distance beyond the bundle, and may be compared with the accessory transfusion tissue in *Cycas*.

A prolific development of lignified elements is seen in various regions in *Welwitschia*, for instance, at the termination of the staminal traces and in the peduncles. Throughout the peduncle of the male inflorescence and at the base of that of the female, the whole pith is composed of elements with lignified walls. Groups of smaller lignified elements also occur in a position centripetal to the protoxylem of the bundles of the peduncles, especially of the outer ring; they are very obvious in the immature ground tissue of most of the female peduncles examined, and are generally found to represent the reduced continuation of inversely orientated bundles.

In many cases when a pair of bundles are found with their xylems directed towards one another (p. 194, Dia. VI) the mass of lignified elements between them contains some tracheides; I am inclined to think that these elements must be here regarded as the homologue of the centripetal xylem seen in connection with the cotyledon bundles, and that they may be compared with the centripetal xylem found in Cycadean peduncles.‡ WORSDELL,§ however, regards the groups of lignified elements throughout the peduncles, and possibly also the whole of the lignified pith, as representing tissue which was originally xylem. The gradual transition found between the elements of the pith and those of the centripetal xylem is a fact which supports this suggestion; but I am inclined to think that the development of lignified elements in the ground tissue of both peduncles, as well as those found

* *Ante*, p. 183; SYKES, M. G., 1910, p. 346.

† *Cf.* SCHEIT, who considers that the origin of the transfusion tissue is always in the xylem (*ex* WORSDELL, 1897, p. 303).

‡ SCOTT, D. H., 1897.

§ WORSDELL, 1901, pp. 768-769.

surrounding the mucilage cavities in the cortex, is probably conditioned by the mechanical necessities of the organs concerned, and it is difficult to draw theoretical conclusions concerning it. MATTE* finds that the centripetal wood in the ovuliferous scales of Cycads passes over into transfusion tissue which may spread in a ring round the bundles. In a similar way the lignified elements internal to the protoxylem and external to the phloem in the bundles of the Welwitschian peduncles have been seen to pass over at a higher level into complete bundles and at a lower level into transfusion tissue. It is questionable, however, if it can be argued from this series of facts that the transfusion tissue in the leaf and bract is homologous with centripetal xylem.

SECTION V.—RELATIONSHIPS OF *Welwitschia*.

A. The relation between *Welwitschia* and other members of the Gnetales would not appear to be very close. The ovule of *Gnetum africanum*† has some characters probably more primitive than are found in either *Ephedra* or *Welwitschia*, but in its gametophyte *Ephedra* is the most primitive of the three. As so much work on these genera is at this present time in course of preparation it would seem inadvisable here to discuss this question further.

On the other hand recent anatomical investigations have brought to light various points of correspondence both between the Gnetales and the present Cycadales, and between the Gnetales and the Bennettitales, while at the same time it appears possible from PEARSON's cytological researches on *Welwitschia*‡ that the embryo-sac in this genus may be regarded as closely related to that of the Angiosperms, and perhaps also to that of the Bennettitales.§ The available evidence seems to point to the connection of the Gnetales with the Cycadalean-Bennettitalean alliance,|| and to the conclusion that the ancestry of the Angiosperms was in some way connected with this alliance.

B. *Comparison between Welwitschia and the Cycads*.—This investigation has brought out numerous points of striking resemblance between the vascular anatomy of the inflorescences and cones of the Cycads and *Welwitschia*. The resemblance, carried as it is into minute details, such as the method of origin of the double bundles supplying the ovuliferous scales of the one and the bracts and flowers of the other, the presence of centripetal wood and inversely orientated bundles in connection with the bundles of the peduncles, and the occasional development of normal concentric bundles in various regions, makes it natural to search for some relation

* MATTE, H., p. 159.

† THODAY, M. G. (SYKES, M. G.), Brit. Ass. Sheffield Meeting, 1910.

‡ PEARSON, 1909.

§ *Ibid.*, p. 386.

|| HALLIER has, however, quite recently attempted to place the Gnetales among the Angiosperms, and has allied them with the Loranthaceæ, 'New Phyt.,' 1905, p. 386.

between these forms. Further, an investigation of the seedling anatomy of *Welwitschia** has revealed other points of comparison with the Cycads.

On the other hand, the foliar position of the ovule and microsporangium in the Cycads must be contrasted with the apparently axillary position of the ovule and characteristic male flower in *Welwitschia*.†

In view of other resemblances it seems to me possible that this difference in the position of the ovule may be regarded as secondary; and each bract with its axillary ovule in the female cone of *Welwitschia* may be homologised with an ovuliferous scale of such a plant as *Dioon*. In the former case, as in the latter, both scale and ovule have a common vascular supply, but, as in the Cycads, it always arises from the same bundle in the stele, and sometimes the two traces arise together from the stele and become free from each other later. In *Gnetum*‡ the bundles which supply the flower and bract have their origin in a common bundle which runs for some way in the cortex before branching. Such an arrangement supports the hypothesis that the ovule (female flower), now borne in the axil of a bract, represents a sorus which was originally borne *on* the bract.

In *Cycas* the seed is probably derived from a sorus consisting of only one fertile sporangium and is produced on the unmodified leaf, while in the other Cycads two such female sori are commonly associated with the specialised ovuliferous scale. In *Welwitschia* it may be that the single ovule or female sorus was originally placed as in the Cycads, the bract being then equivalent to the ovuliferous scale, but secondarily separated from the sorus in connection with it.

The male flowers are rather more difficult to homologise. The argument for regarding the individual male and female flowers in *Welwitschia* as homologous has been stated above. For this and other reasons, I cannot support the view which regards the imperfectly hermaphrodite flower as derived by reduction from an amphisporangiate strobilus.§ In the Cycads the male sporophyll bears a number of sori, and it appears possible that the male flower in *Welwitschia* is also derived from a form in which the sporophyll bore several sori. The fertile scale is now metamorphosed into the bract, while the aggregation of placentæ or sporangiophores|| bearing the several sori has given rise to the male "flower," which consists of a central sorus of one aborted megasporangium, and six peripheral stalked synangia, probably each originally equivalent to a sorus. The megasporangium may not necessarily have ever been fertile. As at the present time we do not know any form among the Cycadean alliance in which both kinds of sori occur on the same sporophyll, this suggestion can only be tentative.

* SYKES, M. G., Linn. Soc., April 21, 1910; Linn. Trans. 1910 (*in ed.*)

† Compare pp. 206-7; the occurrence of anomalous megaspores in the axis of the female cone has been taken as an argument for the cauline nature of the ovule in *Welwitschia*.

‡ STRASBURGER, 1879, p. 106, and figs. 65, 67, Plate 14.

§ STRASBURGER, 1872, p. 153; WIELAND; ARBER and PARKIN, 1908; PEARSON, 1909.

|| BENSON, M. C., 'New Phyt.', 1908.

C. *Comparison between Welwitschia and the Bennettitales.*—The remarkable resemblance in general form and branching between the inflorescences of *Welwitschia* and *Williamsonia angustifolia* has already been pointed out.* The position of the cone in these two genera suggests that the amphisporangiate strobilus characteristic of the Bennettitales is comparable with a telescoped *Welwitschia* cone, and other evidence supports this hypothesis. Many of the peculiarities of the ovulate strobilus of *Bennettites* are explicable as due to the changes which have been involved in the telescoping process. The flattening of the receptacle, bringing into close contact the numerous scales, is the simplest explanation of the extraordinary elongation of the ovular stalk which would then become necessary in order to bring about the exposure of the ovular tips.

While thus regarding the inflorescence of *Welwitschia* as more primitive in general form than that of the Bennettitales, there can also be no doubt that its ovule is nearer to those of the ancient Gymnosperms, with some of which it has been seen that it can be closely compared. The complex vascular system in the ovule of this species is by no means reconcilable with any hypothesis which regards the Gnetales as derived by reduction from such forms as the Bennettitales.†

In the absence of more complete information concerning the ovular vascular supply and other matters,‡ it is difficult to interpret the Bennettitean ovule, but in its elongated micropylar tube and nucellar beak§ it clearly resembles that of *Welwitschia*. The differences between the two, the long pedicel, the possibly reduced outer integument|| and the very simple concentric bundle-supply of the ovule, may be due to reduction and adaptation to the position of the ovule in the telescoped strobilus. The several wings on the covering of the ovule are probably correlated with its position among the surrounding scales, just as the two wings and bilateral structure of the Welwitschian outer integument are correlated with the position of the ovule closely appressed in the axil of a bract.

The ovule with its long stalk would thus be homologous with the shortly stalked female flower of *Welwitschia*, and I should regard some at any rate of the intraseminal scales in *Bennettites* as the equivalent of the bracts in *Welwitschia* and probably of the ovuliferous scales in the Cycads. The scales are here of course more numerous than the ovules, and it is probable that some of them were sterile. The argument which has already been advanced¶ for the primitively foliar origin of the ovule in *Welwitschia* and has consequently been extended to the Bennettitales, receives further support from the fact that the microsporangia in the latter are obviously foliar, and are thus more primitive in character than the stalked microsporangia in *Welwitschia*.

* *Ante*, p. 205.

† ARBER and PARKIN, 1908, p. 497; PEARSON, 1909, p. 338.

‡ LIGNIER, 1894; WIELAND, 1906.

§ Possibly also in the structure of the embryo-sac, PEARSON, 1909, p. 386.

|| PEARSON, 1909, p. 337.

¶ *Ante*, p. 216.

A comparison, on a somewhat different basis, has been made by Pearson,* who compares the Bennettitean strobilus on the one hand with the female cone, on the other with the separate male flowers of *Welwitschia*. The ring of sporangium-bearing organs in the male flower has previously also been compared with the disc-bearing microsporophylls at the base of the strobilus in *Bennettites*.† If, however, on the ground of the anatomical evidence given above,‡ we regard the male and female cones in *Welwitschia* as homologous, we cannot compare the strobilus of *Bennettites* both with the whole female strobilus and with the structures in the axils of the bracts of the male strobilus. It seems more probable that *Bennettites* was derived from the strobilus of some allied plant in which male flowers occurred at the base and female flowers at the apex of the same cone. Such a structure as the male spike of *Gnetum*, at the apex of which female flowers are often present, assists us to realise the probability of bi-sexual spikes having occurred§ in some ancestor from which the Bennettitean amphisporangiate strobilus has been evolved.

D. *Comparison between the Gnetales and the Angiosperms*.—Several recent writers have discussed the possible origin of the Angiosperms from the Bennettitales or Gnetales. All that can at present be said definitely on the question is that our available evidence is in favour of the hypothesis that they are derived from some near ally of both these groups. The embryo-sac characters now held to be common to the two groups were probably shared by this ally, but as more evidence accumulates|| in favour of regarding the Ranales group as the most primitive of living Angiosperms, it appears likely that the inflorescence and flower of the primitive Angiosperms were more closely similar to those of the Bennettitales than to that of the Gnetales. The inflorescence of the Gnetales is too complex to be closely compared with that of any Angiosperm which is likely to be primitive, and the value of PEARSON'S analogy with *Peperomia*¶ is now diminished, since the more thorough investigation of that form has shown that its embryo-sac must be regarded as reduced rather than primitive.**

The ovule of *Welwitschia* seems to me to present several characters which are intermediate between such a seed as *Lagenostoma* and the ovule of the Angiosperms. Two integuments are commonly found in all these forms,†† and in each case the nucellus projects for some distance beyond the level of insertion of the inner integument. In *Welwitschia* the apex of the nucellus is prolonged into a beak; in the Angiosperms it is enlarged to form a spacious brood chamber for the embryo, a

* PEARSON, 1909, pp. 336–338.

† WIELAND, 1906, p. 245.

‡ Pp. 188–190, 196–7, 200–3, etc.; 206–7.

§ Cf. BENSON, 1904, pp. 49–51.

|| SARGENT, 1908; ARBER and PARKIN, 1907 and 1908.

¶ PEARSON, 1909, pp. 341–342; pp. 378–384.

** BROWN, 1908.

†† V. PAYER, 'Organogénie de la Fleur'; BENSON and WELSFORD, 1909, p. 628, etc.

development which is already foreshadowed in *Welwitschia*, where the embryo-sac projects for some distance into the lower portion of the nucellar beak.

In *Welwitschia* the double vascular system of *Lagenostoma* is much reduced, the bundles of the inner integument dying out at the level at which it becomes free from the integument. In the Angiosperms it is only in exceptional cases that the vascular system of the ovule is prolonged beyond the base of the ovule. In *Myrica*,* etc., the single integument is traversed by a well-developed system of bundles. It would appear probable from a comparison with other members of the order† that this single integument represents the two integuments of allied forms fused. BENSON and WELSFORD have already compared the vascular bundles in the integument of such a seed with the system traversing the cupule in *Lagenostoma*. *Welwitschia* seems to me to form a connecting link between the two—*Lagenostoma*, in which the inner system also is fully developed, and the Angiosperms, in which the inner system is generally reduced to form part of the cup of tracheides at the base of the ovule.

In some members of the Euphorbiaceæ‡ the inner integument is fused for some distance with the nucellus and also has a vascular supply. Such an arrangement is in these species probably a specialised development rather than a primitive character, but it is clear that it is very suggestive of seeds like *Welwitschia* and *Lagenostoma*.

The carpel of the Angiosperms§ is, perhaps, traceable to the same origin as the structures which gave rise to the bract of *Welwitschia*, and the interseminal scale of the Bennettitales, having here become secondarily adapted for the enclosure of the ovule may be in connection with insect pollination.|| It is probable, however, that the Angiosperms are derived from a group of forms in one respect more primitive than either of these, in which the ovules were still borne on the sporophyll,¶ which has since closed round them to form the carpel. These ancestors may have already evolved a telescoped strobilus, such as is found in the Bennettitales, while changes were taking place in the development of the gametophyte, stages of which are possibly preserved in both *Welwitschia* and the *Bennettitales*.

SECTION VI.—SUMMARY AND CONCLUSIONS.

1. In the *cotyledons*, the young and old foliage *leaves* and the young and old *bracts*, the development of the xylem is centrifugal, except for a small number of centripetal elements at the base of the two main bundles of the cotyledon. The sheath of transfusion tissue, which more or less surrounds the bundles in all the foliar members, is situated in the pericycle, and shows no sign of having been derived from the xylem; in the bracts, and to a smaller extent in the old leaves, there is a further

* KERSHAW, 1909.

† BENSON and WELSFORD, 1900, p. 628.

‡ LE MONNIER, 1872.

§ Cf. OLIVER, 1906, p. 239; PEARSON, 1909, p. 341.

|| See ROBERTSON, C., 1904; BESSEY, 1897; ARBER and PARKIN, 1907.

¶ WORSDELL, 1905; ARBER and PARKIN, 1908; BENSON and WELSFORD, 1909,

development of transfusion-tissue elements from the cortical parenchyma. The bracts of the adult male and female cones are essentially similar in structure, one to the other.

2. The structure of the naked inflorescence axes is found to be extremely complex. The bundles are arranged in two more or less definite series. At each point of branching two bundles enter from each of the two bracts and a number of bundles from the buds or lateral axes in their axils. A series of elongated and waved masses of vascular tissue are formed below this level; they generally consist of bands of normally orientated xylem and phloem, with an inversely orientated band on its outer edge, that is, there are two adjacent parallel bands of phloem with xylem on either side. Such a structure recalls the vascular anatomy of *Colpoxylon*, and others of the Medulloseæ, but the xylem and phloem have there the reverse arrangement. Normally concentric bundles are also found at this level. Lower down the waved bands break up into portions, on the outer and inner edges of which are inversely orientated bundles recalling those described in the Cycads. These persist for some length of time, and at a lower level either fuse with the larger normally orientated bundles or die out slowly. In the latter case they are for some time represented by a few xylem elements, which on the inner side of the bundles occupy a position centripetal to the normal xylem; there are often other tracheides more or less surrounding the normal bundles, and sometimes forming an incomplete sheath of elements in appearance recalling the transfusion-tissue sheath in the leaves. From their derivation it is, however, clear that, in the peduncles, this sheath represents the remnant of the inverse series of bundles.

Centripetal xylem is also found in some portions of the peduncle; a gradual transition can be traced from the protoxylem through the centripetal xylem to the lignified pith of the male peduncle. In the female inflorescence the pith is lignified only at the extreme base.

3. The *rachis of the cones*, both male and female, is traversed by four arcs of bundles, connected in the female by some smaller accessory bundles. From the bundles at the two corners of each arc pairs of branches arise which supply the cone bracts. From the same bundles at a slightly higher level two more bundles arise; these, together with a contribution from the bundles at the corners of the adjoining arcs in the male cone, or from an accessory bundle in the female, supply the stalks of the flowers. After thus supplying several bracts and flowers, the corner bundles pass out entire, and their place is filled and the original number restored by the branching of the other bundles of the arc.

4. The traces which supply *the female flower* often become concentric on their way through the cortex. On entering the flower stalk six bundles are formed by the branching of the pair. Two of them supply the outer integument. The remaining four branch to form a perinucellary ring, generally consisting of eight main bundles, which die out at the level at which the inner integument becomes free. If an arbitrary boundary to the nucellus is obtained by prolonging downwards

the line of separation of the free regions of the nucellus and integument, then the inner system is seen to belong to the integument.

The inner integument and nucellar beak are very much elongated, and the margin of the micropylar tube is strongly cuticularised. The embryo-sac generally extends upwards for a short distance into the free portion of the nucellus, and downwards to the level of origin of the outer integument.

5. In the *male flower axis* the branching of the bundles is similar to that in the female, but at each fork a median trace is also formed which supplies a stamen, while the lateral ones run on in the flower-axis. A reduced ring of bundles is present at the base of the ovule; two large lateral bundles are conspicuous among the others, and probably represent the reduced vascular supply of the single integument which is here regarded as representing the outer integument of the female flower.

6. An interesting *abnormal female flower* is described, in which an outgrowth is formed from the outer integument; this outgrowth arises from one side only, is free in its upper portion, and persists up to the level of the nucellar tip.

7. It is concluded, from a study of the vascular structure, that *the male and female inflorescences, cones, and flowers are homologous*.

8. It is thought probable that *Welwitschia* is not very closely allied to the other Gnetales. *A comparison is made with the Cycads, the Bennettitales and the Angiosperms.*

Various characteristics of its vascular system, the double trace supplying its appendages, the concentric and inversely orientated bundles in the peduncle and cones, the mesarch xylem at the base of the cotyledonary traces, connect *Welwitschia* with the Cycads and the Medulloseæ. In general form and branching, the inflorescences resemble most closely those of *Williamsonia angustifolia*.

It is suggested that the *Williamsonia* strobilus not only resembles that of *Welwitschia* in position, but that it is really derived from the bisexual spike of a similar, but more primitive form, by a telescoping process. *Williamsonia angustifolia* represents possibly an intermediate stage in the process. Some such hypothesis explains most naturally the peculiarities of the ovule of the Bennettitales, obviously far less primitive than those of the Gnetales.

9. The ovules of the Cycads, and probably the primitive Angiosperms, are foliar, while those of the Gnetales and Bennettitales have been commonly regarded as cauline. The suggestion is made that, although the ovules in the female cone and the stamens and aborted *ovules* in the male cone are now in an axillary position, they *may not originally have been cauline*. The anatomy of the peduncles and cones, and the vascular supply of the scales and ovules, is so strikingly like that of the Cycads that it is impossible to avoid the impression that there is here more than analogy. It seems not unreasonable to suppose that the sorus receptacle has here secondarily taken up an axillary position, and that the bundles supplying its base have therefore become inserted lower on the bract bundles than in the Cycads.

There are points of striking similarity between the ovules of *Welwitschia* and *Bennettites*. In *Bennettites* the microsporangia are foliar, a fact which seems to suggest that the megasporangia are also primitively foliar.

The bracts of *Welwitschia* are thus compared with the carpels of the Angiosperms, the interseminal scales of *Bennettites*, and the ovuliferous scales of the Cycads.

10. The ovule of *Welwitschia* appears to have some remarkably primitive characters. It consists of a nucellus, with two integuments, each of which has a vascular system. It is thus closely comparable with *Lagenostoma*. The attempt is made to show that *the primitive form of seed throughout the alliance* consisted of a nucellus fused with an inner covering, which was free only in its upper region, and enclosed in an outer covering free to the base, and having a double vascular system supplying the two integuments. In *Cardiocarpus* and the Cycads the two integuments are fused, but in both, as in *Lagenostoma*, the vascular system is regarded as entirely integumental. The seeds of the Gnetales must have been derived very early from the base of the Cycadean series, for there is no sign of fusion between the two integuments.

11. It is suggested that still further abortion of the vascular system and the *continued upward growth of the nucellus* would lead to the formation of such an ovule as we find in the Angiosperms. Exceptional cases among the Angiosperms, in which the vascular system of the outer integument is preserved, form interesting indications of intermediate stages. Recent evidence is in favour of regarding the Angiosperms as derived from some near ally or ancestor of the Gnetales and Bennettitales, which possessed the embryo-sac characters probably common to both, in conjunction, perhaps, with a telescoped strobilus, and a simple ovule with two integuments, the nucellus of which was well developed in its upper portion.

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- Idem.* "A Study of the Vascular System in Certain Orders of the Ranales," 'Annals of Botany,' 1908.

DESCRIPTION OF PLATES.

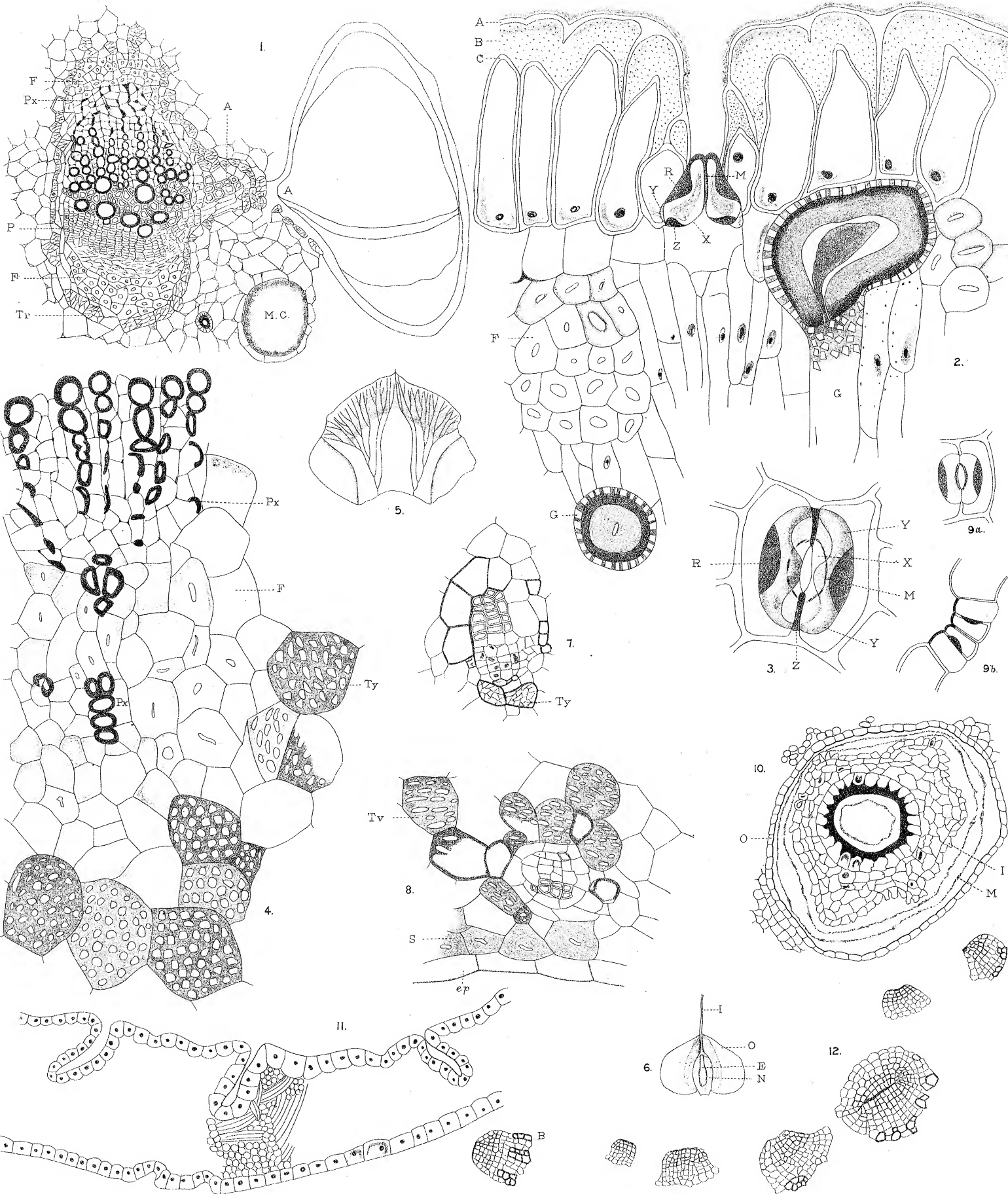
PLATE 17.

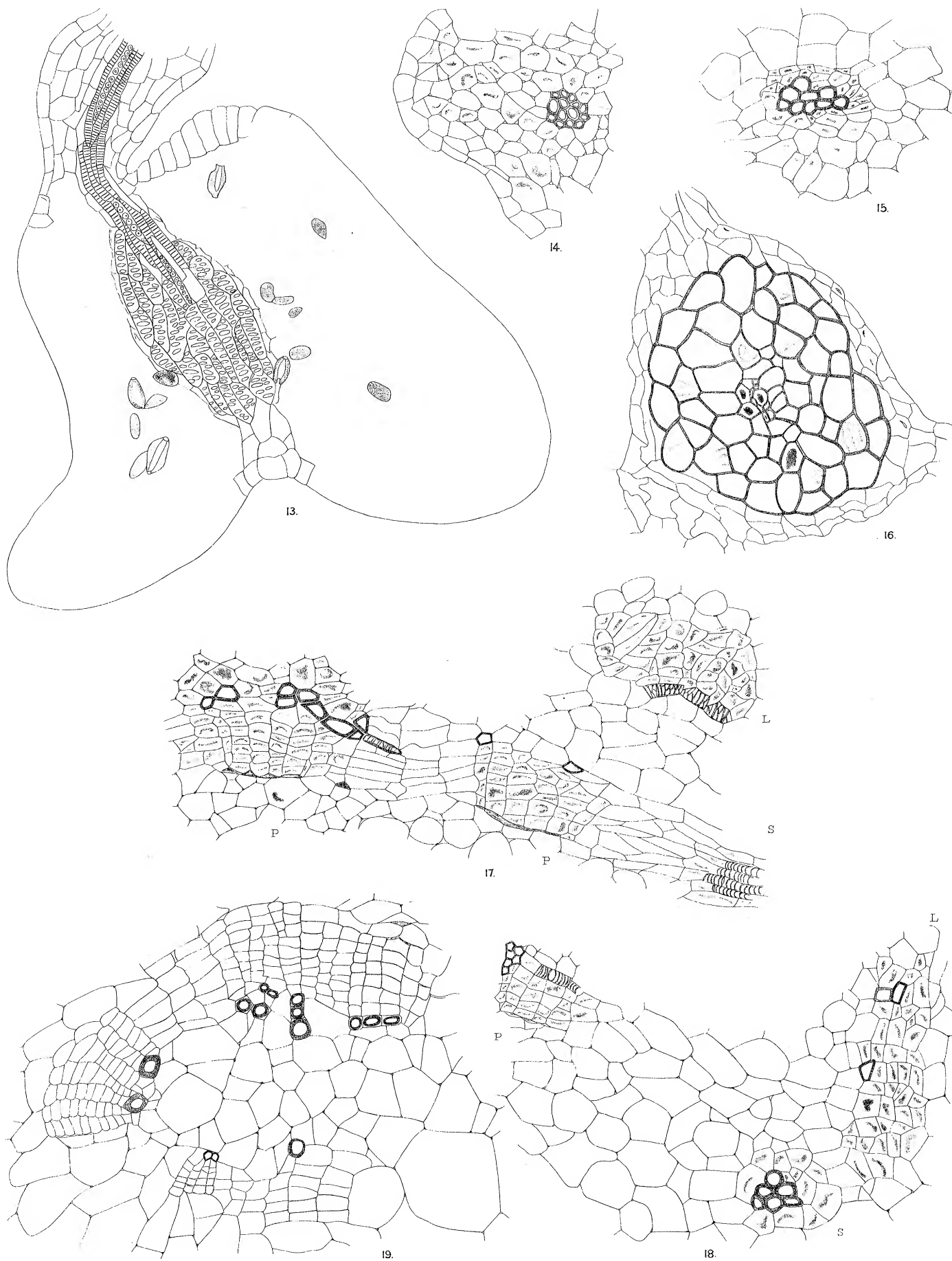
- Fig. 1.—Two bundles of an adult leaf seen in transverse section. Between the bundles is a mucilage canal. (The phloem is somewhat crushed and therefore not satisfactorily represented.) $\times 78$. (F, fibres; *px*, protoxylem; *p*, phloem; Tr, transfusion tissue; A A, Anastomosing bundles; M, mucilage canal.)
- Fig. 2.—A small portion of a transverse section of the leaf. $\times 116$. For a description of both these figures, see text, pp. 180–2. (A, B, C, three layers of outer wall of epidermal cell; G, branched lignified fibre; F, sclerenchymatous fibres; other letters as in fig. 3 (see text).)
- Fig. 3.—Stoma of adult foliage leaf, seen from below. The cuticularised portions are represented black, while the thickened but uncuticularised area is more faintly shaded. $\times 116$.
- Fig. 4.—The upper portion of a leaf bundle in transverse section. A cap of sclerenchymatous fibres (F) is seen above the bundle and a portion of the sheath of transfusion tissue (Tr) is shown. The protoxylem (*px*) is much crushed except in the case of a few elements which are surrounded by the fibres. $\times 116$.
- Fig. 5.—Bract from female cone, showing course of bundles. $\times 2$.
- Fig. 6.—Ovule which was appressed in the axil of bract. This was the most mature specimen among my material. O, winged outer covering; I, projecting tube of inner covering; N, nucellus.

- Fig. 7.—Single bundle from cotyledon, seen in transverse section. The cells of the transfusion sheath (Ty) are hardly yet lignified, and sclerenchymatous fibres are absent. $\times 116$.
- Fig. 8.—Single bundle from bract of male cone. Tr, cells with lignified pitted walls formed from ground tissue; S, sclerenchymatous fibres; ep, epidermis of inner surface of bract. $\times 78$.
- Fig. 9.—Stoma of bract in section (b) and seen from below (a). $\times 116$.
- Fig. 10.—Transverse section through the apical region of the female flower. m, mucilage; o, outer integument or “perigone;” i, inner integument; the innermost ring is the micropylar tube with its cuticularised lining. $\times 116$.
- Fig. 11.—Transverse section of part of the winged “perigone” of a female flower; this is an unusual specimen and shows a number of deep grooves on its inner surface. $\times 78$.
- Fig. 12.—Transverse section of female cone, showing part of one arc of bundles. B represents a corner bundle which will pass out to the next bract. One of the bundles is inversely concentric. $\times 78$.

PLATE 18.

- Fig. 13.—Longitudinal section of a stamen showing the vascular bundle ending in a mass of cells with lignified pitted walls. $\times 78$.
- Fig. 14.—Transverse section of base of a stamen stalk; the bundle is here seen to be concentric. $\times 116$. (Cf. bundle in *Bennettites* pedicel.)
- Fig. 15.—As 14, taken at a level higher up the stalk. $\times 116$.
- Fig. 16.—Transverse section through the apical region of a stamen, passing through the septum in the anther, and showing the transfusion tissue.
- Fig. 17.—Transverse section of axis of male flower, at about level F. in Dia. II, p. 189. Shows two posterior bundles (PP). One staminal trace (S), with the inversely orientated bundle (L), has arisen by the branching into three portions of one of the posterior bundles. $\times 116$.
- Fig. 18.—As 17, but higher up in the axis. Here the bundle L is at its fullest stage of development, above this level it dies away. $\times 116$.
- Fig. 19.—Transverse section through one of the bundles supplying the axis of the female flower as it passes out through the cortex of the rachis. Here it is clearly concentric. $\times 116$.





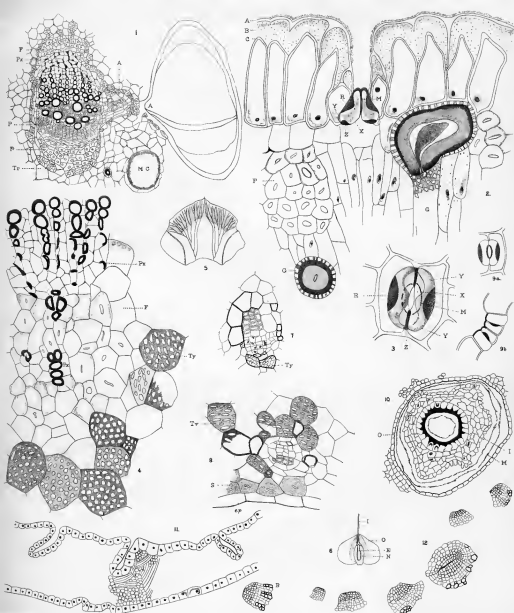


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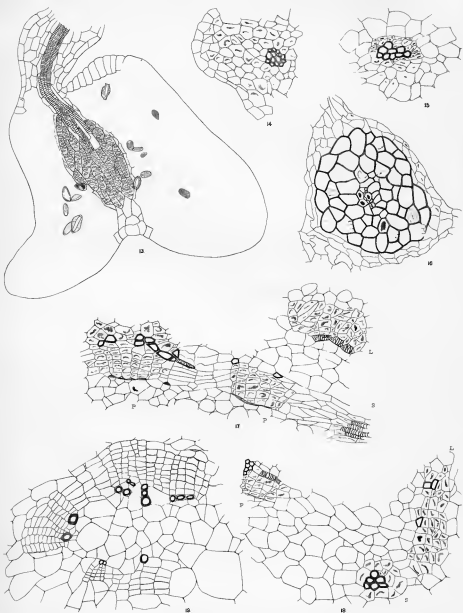


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